The Invasive *Ailanthus altissima* in Pennsylvania: A Case Study Elucidating Species Introduction, Migration, Invasion, and Growth Patterns in the Northeastern US

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The Invasive *Ailanthus altissima* in Pennsylvania: A Case Study Elucidating Species Introduction, Migration, Invasion, and Growth Patterns in the Northeastern US

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Abstract - *Ailanthus altissima* (Tree of Heaven), an invasive tree species native to China and East Asia, was first introduced into the US ca. 1784 by William Hamilton at his Philadelphia, PA estate. However, the means and temporal progression of spread from this and other early points of introduction are not clear. This species now occurs in >40 US states, primarily as an urban and roadside weed. The Northeast supports the highest densities of *Ailanthus* within the US, mainly in transportation corridors and urban areas, where it has become the dominant tree species. A recent, widespread increase in *Ailanthus* incidence in eastern hardwood forests, not unlike prior invasions along railways and roadsides, suggests that current conditions favor invasion in natural environments. To help elucidate the life history of *Ailanthus* in Pennsylvania and the northeastern US, as well as answer fundamental biological questions concerning this species, we conducted dendrochronological (tree-ring) studies and floristic surveys beginning in 2010. Although we studied population dynamics, age structure, and tree-ring characteristics of *Ailanthus* primarily in Pennsylvania, we supplemented our studies using trees from adjacent northeastern states. Floristic studies, conducted between 2010 and 2011, revealed *Ailanthus* to be present in 60 of 67 Pennsylvania counties, including nine previously unreported counties. Tree-ring studies of these trees, as well as of trees from adjacent states, indicated *Ailanthus* was a suitable species for tree-ring analyses, although false rings were observed in >20% of trees examined. Our results also revealed *Ailanthus* to be longer-lived than previously reported, reaching ages >100 years, at which time female trees still produced viable seed. However, extant *Ailanthus* did not exceed 120 years in age, and therefore could not be directly linked with any documented late 18th-century or early 19th-century plantings. Nevertheless, continuous colonization in southeastern Pennsylvania, spanning two centuries, by overlapping generations of *Ailanthus* was supported by observations at Bartram's garden in Philadelphia. Regression analysis revealed that tree diameter was a significant predictor ($R^2 = 0.80$) of *Ailanthus* age and could be used to estimate ages of historic trees whose diameters were reported in early literature, which revealed establishment of *Ailanthus* in six Pennsylvania counties 70–118 years earlier than previously reported. Tree-ring studies of extant trees revealed that *Ailanthus* had gone unreported in some counties for 50 years, during which subsequent invasions occurred. Lastly, we report that widespread invasion of forests by *Ailanthus* is a relatively recent phenomenon in Pennsylvania, with most invasions occurring after 1965, following major forest disturbances such as salvage logging in the aftermath of widespread insect defoliator outbreaks, especially *Lymantria dispar* (Gypsy Moth) defoliations. These findings are consistent with previously reported lag times between initial colonization and the onset of rapid range expansion for other invasive plant species. Our results emphasize the need

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for more thorough inventories of *Ailanthus* within forests prior to harvesting. Such inventories will afford forest managers opportunities to preemptively eradicate *Ailanthus* and mitigate future invasions by this species.

Introduction

Early introductions and observations of *Ailanthus* in the Northeast

Ailanthus altissima (Mill.) Swing. (formerly *A. glandulosa* Desf.) (Tree of Heaven), hereafter called *Ailanthus*, was first introduced into the US from its native China via England in 1784 or 1785 by William Hamilton at his country estate "The Woodlands" (currently the Woodlands Cemetery) in Philadelphia, PA (Browne 1846, Carr 1861, Dwight 1845). A second introduction into the northeastern US occurred in 1804 in Portsmouth, RI, directly from China (Browne 1846, Prince 1827). Despite these early introductions into the northeastern US, it wasn't until several decades later that *Ailanthus* became widely available in the horticultural trade: first and foremost by Prince Nursery (Flushing, Long Island, NY) in 1820, followed by Bartram's Garden (Philadelphia, PA) in ca. 1828 (Browne 1846, Carr 1828).

Widespread adoption of *Ailanthus* by nurserymen and gardeners after 1820 was likely due to the presence of seed-bearing *Ailanthus*, which allowed trade in seed and seedlings rather than cuttings. Indeed, the earliest evidence of seed production by *Ailanthus* in the US is found in an undated herbarium specimen from the Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia (PH) collected by Solomon W. Conrad in Philadelphia between 1815 and 1831 (Fig. 1a, cover). Given the rarity of *Ailanthus* during this time in Philadelphia, the specimen likely came from Bartram's garden, the only confirmed site of *Ailanthus* cultivation in Philadelphia prior to 1827 in addition to the Woodlands. During this same time period, Conrad had collected other plant species in Bartram's Garden that are also included in collections at the Philadelphia Herbarium (Rabeler 1985). Procurement of *Ailanthus* at Bartram's garden for out-planting at the Philadelphia Cemetery in 1827 support the likelihood of seed propagation at this time (Jones 1835).

A second specimen from Philadelphia, dated 1841, accessioned in the New York Botanical Garden Herbarium (NY Accession No. 785400), represents the earliest, accurately dated seed-bearing *Ailanthus* in the US (Fig. 1b). Other early seed-bearing specimens from surrounding areas include Batsto Village, NJ (1863) and Brooklyn, NY (1866) (NY Accession No. 785391 and Brooklyn Botanical Garden Herbarium [BKL] Accession No. 66572, respectively). Based on these specimens, seed-bearing *Ailanthus* were not likely present before 1820, since *Ailanthus* seed had not been previously reported or found in any extant US herbaria collections. Moreover, *Ailanthus* trees <10 years of age can bear seed, which would have given this species ample opportunity to sexually reproduce, had both gynoecious (seed-producing) and androecious (pollen-producing) plants been present in the areas of early introduction (Dwight 1845, Miller 1835). The earliest reports of seed-bearing *Ailanthus* in Pennsylvania (PA) were first published in 1846 (Browne 1846) and with specific reference to Bartram's garden in 1855 (Barry and Smith 1855). By 1868, *Ailanthus*' ability to spread from seed in PA, and presumably elsewhere, was widely acknowledged (Gray 1868b). One explanation for the absence of sexual reproduction during the first decades following introduction comes from Monson (1843), who explained that *Ailanthus* planted in cities during the early 19th century were mainly cuttings from a single "variety" that did not produce seed.

In Philadelphia, prior to seed cultivation by Bartram and other nurserymen, *Ailanthus* were propagated exclusively by cuttings from Hamilton's original staminate trees (Browne 1846, Dwight 1845, JBA 1907). Herbarium specimens from England's earliest points of introduction (ca. 1751), Chelsea Botanic Garden,and Philip C. Webb's private exotic gardens at Busbridge in Surrey near London, support the pervasiveness of staminate *Ailanthus* during the time period when

Figure 1. A) Earliest known *Ailanthus altissima* herbarium specimen in the US containing seed. Collected by S.W. Conrad, Philadelphia, Philadelphia County, PA, between 1815–1831 (Philadelphia Herbarium at the Academy of Natural Sciences, Accession No. 01097312). Notes: Decand. trigynia (polygam), S.W. Conrad. Although undated, this specimen includes Conrad's pre-printed commercial labels that he began using after 1815 (Wilson 2011). Conrad used Linnaean classification to identify the plant. Conrad's classification was later supported by a formal botanical description of *Ailanthus* (Gray 1868a). Printed with permission of the Academy of Natural Sciences, Philadelphia B) Earliest accurately dated US *Ailanthus altissima* herbarium specimen containing seed, Collected by J.P. James, Philadelphia, Philadelphia County, PA, August 1841 (New York Botanical Garden Herbarium, Accession No. 785400). Notes: Ex Herb. J.M. Coulter, Incorporated Herbarium: Herbarium of Wabash College. Printed with permission of the New York Botanical Garden Herbarium.

Hamilton's *Ailanthus* was acquired from England (Loudon 1844, Miller 1835) (Natural History Museum, London Accession No. BM001017992). Despite the ease of propagation, Hamilton apparently disseminated few of his *Ailanthus* plants. Hamilton jealously guarded these rare exotic plants, since he went to considerable risk and trouble to procure and import them to the US (Browne 1846, Downing 1844). In a letter to his secretary Benjamin H. Smith (dated 12 June 1790), Hamilton wrote, "It would have been an agreeable circumstance to me to have heard the large sumachs [*sic*, *Ailanthus*] and Lombardy poplars … have not been neglected. After the immense pains I took in removing the exotics to the north front of the house, by way of experiment, you will naturally suppose me anxious to know [their] success … and the effect as to [their] appearance in approach …" (Smith 1905b). In another letter, Hamilton emphasized that plants "… should be kept in the Hot House under lock and key … [and] nobody … should get sight of them …" (Smith 1905a). Consequently, only Hamilton's horticulturally minded contemporaries including Humphrey Marshall and William Bartram ever received *Ailanthus* cuttings from Hamilton, and only after sharing plants from their own collections (Browne 1846, Darlington 1849).

In 1809, Bartram received an *Ailanthus* sucker sprout from Hamilton. By 1877, the sprout had grown to a sizable 90.7 cm in diameter at breast height

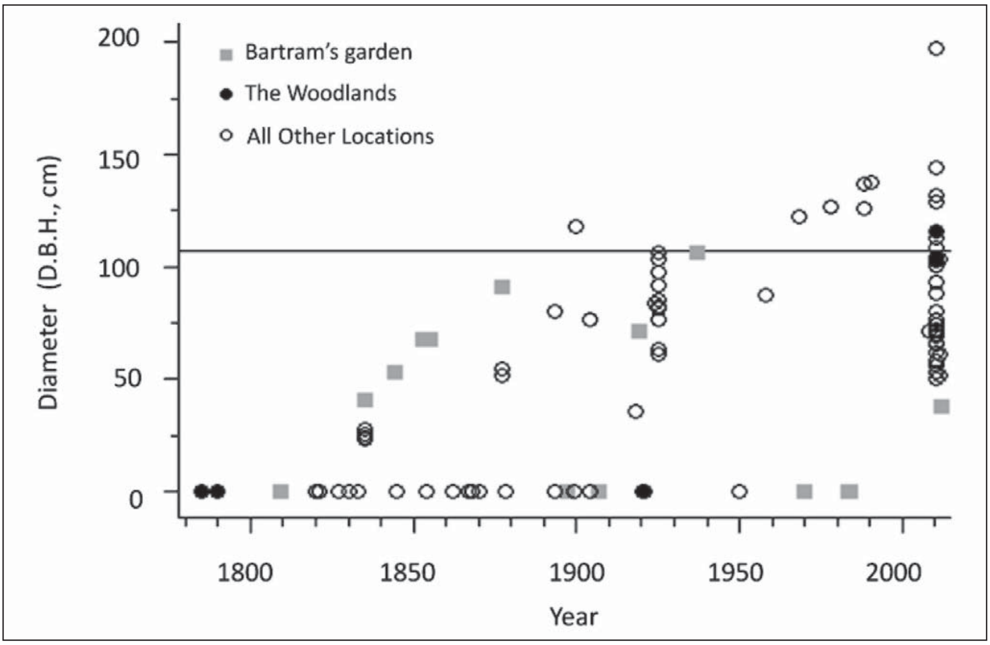

Figure 2. Historical measurements of *Ailanthus* trees found throughout PA from time of introduction through 2010. A value of 0.0 was given for trees with a known planting date and for individuals whose measurements were excluded from a specific reference but contained, in many cases, a qualitative description. Reference line at 107 cm denotes the maximum diameter previously reported for *Ailanthus* (Miller 1990). Some individual observations represent more than one tree. Other denotes both historic and non-historic locations and includes observations across ten PA counties (See Appendix 2 for complete list of references).

(DBH: diameter at 1.4 m; Fig. 2; Browne 1846, Sargent 1878). Observations in Marshall's arboretum ca. 1893 revealed "… a very large *Ailanthus*, which must have been one of the first specimens planted in America [and] seems to date from the time of Marshall," ca. early 19th century (Sargent 1893). Although the diameter of Marshall's *Ailanthus* in 1888 was not reported, comparisons to other old trees measured in Marshall's arboretum in 1880 allows a conservative estimation of 60–75 cm for Marshall's *Ailanthus* (Fig. 2; Sargent 1880). Further dissemination of Hamilton's *Ailanthus* plants, prior to distribution in the horticultural trade, may have resulted from an 1809 exotic plant sale from Hamilton's extensive collection, or as *Ailanthus* cuttings from Bartram's or Marshall's established specimens (Belden 1958, Darlington 1853, Dwight 1845, Hamilton 1809).

Reports of comparably sized *Ailanthus* trees at the Woodlands through the 19th and 20th century were not found, suggesting that Hamilton's own *Ailanthus* trees were either short–lived and/or cut back purposely to provide a desired aesthetic in his meticulously manicured English garden (Long 1991, Oldschool 1809). A third possibility building on the latter hypothesis, and supported by several accounts including Hamilton's own letters, was that *Ailanthus* trees among other exotics were never out-planted on the grounds of The Woodlands but instead "… were arranged tastefully in large oval grass plats (artificial mounds with various-sized holes for potted plants) in front of the conservatory [to] represent a miniature hill clothed with choice vegetations" (Drayton 1806), after which plants were returned to the greenhouses for the winter (Long 1991, Wunsch 2003). Reports that Bartram and Henry Pratt (Lemon Hill, Fairmont Park, Philadelphia) received *Ailanthus* suckers from Hamilton at the time of the documented plant sale, support the latter hypothesis that some of Hamilton's *Ailanthus* trees were never out-planted, but rather were likely distributed to Hamilton's fellow botanists (Browne 1846, Dwight 1845).

Regardless of uncertainty involving the spatial arrangement and persistence of first-generation *Ailanthus* stems at the Woodlands, Harshberger (1921) observed "… descendants of the first *Ailanthus* tree planted in America …" at the Woodlands in ca. 1920. Whether the *Ailanthus* was established from wind-disseminated seed from off-site, or as sprouts of surviving root systems from first generation plantings, is unknown. Unfortunately, Harshberger reported no additional information regarding *Ailanthus* tree location or size, nor are there any records documenting the original planting sites for *Ailanthus* at the Woodlands.

Commercialization of *Ailanthus*

Shortly after *Ailanthus* became widely available in the horticultural trade, demand for this species surged as evidenced by numerous newspaper advertisements throughout New England and the Mid-Atlantic region, which were absent throughout the 1820s (Anonymous 1833, Manning 1830, Minor 1835, Pavilion 1830, Peirce 1833, Sinclair 1835, Thornburn 1830). This surge in popularity was attributed to *Ailanthus*' noble appearance and tropical-like foliage, hardiness and rapidity of growth, and for its ability to thrive in the poorest soil (Sargent 1888). As testament to the high demand for this species, Bartram's 1828 Garden catalogue listed *Ailanthus* at $1.00 each compared to $0.25 each for *Populus nigra* "Italica" L. (Lombardy Poplar) and $0.50 each for *Aesculus hippocastanum* L. (Horse Chestnut), two other popular imports (Carr 1828). Only *Ginkgo biloba* L. (Ginkgo, Maidenhair Tree), another exotic import credited to Hamilton, and a native, yellow-flowered *Magnolia acuminata* L. (Cucumber Magnolia), demanded a higher price at this time (Carr 1828). More than 15 years later, a report from NY by Dwight (1845) listed *Ailanthus* at $1.50 each for 2-year-old trees, indicating that demand for this species was still very high into the middle of the 19th century.

Although *Ailanthus* gained popularity across smaller cities and towns in the mid-1800s, its notoriety in large cities where it was first introduced became readily apparent. In 1852, A.J. Downing, prominent writer and editor of *The Horticulturist* and *Journal of Rural Art and Rural Taste*, denounced the incurable vices of *Ailanthus*. Downing (1852) spoke out firmly against further planting of *Ailanthus*, insisting it "… fills the air with a heavy, sickening odor, it suckers abominably, and thereby over runs, appropriates and reduces to beggary, all the soil of every open piece of ground where it is planted …" Yet despite the problems with *Ailanthus* in urban centers where it was aggressively planted at the cost of native species, "… country gentlemen, seduced by the oriental beauty of its foliage, continue to plant it in their pleasure grounds" (Downing 1852). Surprisingly, *Ailanthus* is still available (2013) commercially via various online nurseries for as little as $1.50 each for 1–2 foot tall trees.

Intra-state migration, proliferation, and growth of *Ailanthus* in PA

Even with high costs and growing opposition in cities, the incidence of *Ailanthus* throughout PA increased steadily after 1820 (Appendix 1). Concurrently, the incidence of large *Ailanthus* trees (>50 cm DBH) was reported for the first time beginning around 1850 (Fig. 2). By the early 20th century, reports indicate that *Ailanthus* was well distributed throughout the state, suggesting that many of the scattered geographic pockets reported in the mid- to late-1800s of *Ailanthus* had presumably coalesced (Appendix 1). The incidence of larger *Ailanthus* trees (50–120 cm DBH) also increased dramatically in southern PA during this time period, with reports of large *Ailanthus* in Adams, Chester, Cumberland, Dauphin, Franklin, and Philadelphia counties (Fig. 2; Illick and Brouse 1926).

Large trees at Bartram's and Marshall's gardens were, given their growth patterns, likely second-generation root sprouts of *Ailanthus* planted earlier at these same sites (Fig. 2, 3B). Large, first-generation *Ailanthus* trees were reported in Adams, Cumberland, Dauphin, and Franklin counties, further validating species acclimation throughout its new environment (Figs. 2, 3C). Naturalized dense thickets of *Ailanthus* also were observed near Reading (Berks County), Mont Alto (Franklin County), and north of Harrisburg along the Susquehanna River upstream from Clarks Ferry Bridge (Dauphin County) (Illick and Brouse 1926). Reforestation projects using *Ailanthus* seed on denuded industrial lands in western PA by the PA Division of Forests and Waters (now PA Bureau of Forestry) likely hastened *Ailanthus*' expansion into additional disturbed areas of the state (Illick and Brouse 1926).

Over the last half-century, published reports indicate a dramatic increase in counties with confirmed *Ailanthus* (Appendix 1). Yet, during this same time period, the largest *Ailanthus* trees ever recorded in the state were reported from two counties (Lebanon and Wyoming) where *Ailanthus* allegedly had established after 1960 (Fig. 2, Appendix 2; Clark 1988, 1991). The apparent inaccuracies in county-specific incidence reports for *Ailanthus* emphasize the need for further investigation to more firmly resolve spatiotemporal migration patterns. Given the long residency (≈230 years) of this species in the state, it is likely that *Ailanthus* populations may have occurred at low levels (e.g., individual trees) earlier in many additional counties with first reports after 1960, but went unnoticed or unreported.

Invasion of PA forests

It is unclear when *Ailanthus* first became a significant problem on PA forest lands and in rest of the Northeast despite *Ailanthus*' presence as an incidental species in many counties and states for more than a century. Currently, *Ailanthus*

Figure 3. Early photographs of *Ailanthus* trees (white arrows) in PA: A) Krauth House, Lutheran Theological Seminary, Gettysburg ca. 1911–1925; B) Humphrey Marshall's arboretum, Marshallton c. 1925; C) York Springs ca. 1925. The Krauth House trees were two of eight apparently planted at the newly established Seminary during the early to mid-1830s, but were cut down in April 1950 because of declining health. At Marshall's garden there was a group of seven large *Ailanthus* of spout origin ranging from 61–76 cm DBH in ca. 1925. *Ailanthus* was first introduced here before 1820. The last documented *Ailanthus* in Marshall's arboretum was an 86.4-cm-diameter stump in 1958. The *Ailanthus* tree at York Springs was 91.4 cm DBH in 1925. Photo A printed with permission of Lutheran Theological Seminary. Photos B and C reprinted from Illick and Brouse (1926) with permission of the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry.

is one of 25 reported non-indigenous trees and shrub species intentionally introduced into the PA for food, fiber, or ornamental purposes that have escaped cultivation and pose serious, long-term threats to native plant diversity (Morse et al. 1995, PA DCNR 2013). *Ailanthus*' allelopathic properties against 35 deciduous and 34 coniferous native species (Mergen 1959), prolific seed production (Bory and Clair-Maczulajtys 1980), and persistent root suckering (Hu 1979) make it an exceptional invader, particularly in open areas with disturbed mineral soil, where *Ailanthus* easily supplants native species (Rhoads and Block 2007). Successful invasion may be further enhanced by the species' association with endomycorrhizal fungi (Huebner et al. 2007). *Ailanthus* can also exploit small forest gaps where it relies on vegetative reproduction, surviving in the understory as long as 19 years prior to recruitment (Knapp and Canham 2000, Kowarik 1995, Martin et al. 2010).

Because most state and federal forest lands in PA were not established until the early 1900s, *Ailanthus* was likely present on some lands prior to their acquisition by governmental agencies. In addition, some *Ailanthus* were probably intentionally introduced onto public lands as a means of reclaiming post-industrial waste lands (Illick and Brouse 1926).

Data from USDA Forest Service Forest Inventory and Analysis (FIA) plots recently revealed that *Ailanthus* stems increased dramatically in PA forests from 76 million in 1989 to ≈135 million in 2004. These findings suggest that conditions since 1989 favor proliferation of *Ailanthus* in PA forests where this species had been significantly less abundant or previously absent (Alerich 1993, McWilliams et al. 2007). Despite these reported increases in *Ailanthus* stems from 1989 to 2004, data from southeastern PA (SE PA) did not distinguish *Ailanthus* in the 1989 inventory where many stands were identified in the 2004 inventory. Thus, comparisons between the two inventories could not be made. Nevertheless, significant increases did occur where *Ailanthus* was documented in both inventories (Alerich 1993, McWilliams et al. 2007).

Eichelberger and Perles (2009) recently evaluated the status of invasive plant species in the Delaware Water Gap National Recreation Area (DEWA) in PA and New Jersey (NJ). These authors listed *Ailanthus* as a top invasive plant, particularly in shale woodlands, shale scree slopes, and sparsely vegetated cliff areas. Turner et al. (2007) documented recent establishment of *Ailanthus* within the forest understory at the Gordon Natural Area, Chester County, PA, which has occurred since a previous survey in 1970 (Overlease 1973). Similarly, Espenschied-Reilly and Runkle (2008) reported an increase in incidence and size class of *Ailanthus* from 1980 to 2002 within the Wright State University woodlot near Dayton, OH. These observations, among others, reveal a disconcerting trend of increasing invasion by *Ailanthus* into native forests and natural landscapes.

Even in the absence of major disturbances, spread of invasive species such as *Ailanthus* continues to occur in areas adjacent to roadsides (Mortensen et al. 2009). Transportation corridors are ideal for colonization by invasive species due to their open nature, but also due to secondary seed dispersal mediated by vehicular traffic (Aldrich et al. 2010). With continued suburban sprawl and infrastructure expansion, not only will these trends continue but will likely intensify as well.

Persistence of *Ailanthus* on the landscape

Effective control strategies to mitigate further spread of *Ailanthus* are limited by our incomplete understanding of biological processes that enhance survival and proliferation of this species. One key to understanding invasion potential is to answer fundamental questions regarding *Ailanthus* life expectancy and growth patterns. With knowledge of such attributes, we can more accurately reconstruct *Ailanthus* spatiotemporal migration throughout PA and evaluate factors that favored the establishment of extant populations. Such knowledge can ultimately guide management and control efforts in PA where *Ailanthus* has long been established, as well as elsewhere in the US where *Ailanthus* has only recently invaded.

Despite previous reports that *Ailanthus* is short-lived in the northeastern US, ranging from 50–75 years (Jellett 1904, Sargent 1878, Stefferud 1949), dendrochonological (tree-ring) investigations in England (Cutler et al. 1993) and anecdotal evidence in the US (Belden 1958, Sargent 1893, Wentz 1950) suggests that the lifespan of *Ailanthus* likely exceeds 100 years. In southeastern China, *Ailanthus*' country of origin, 70-year-old trees have been reported (Shouxiang et al. 2008). However, no thorough dedrochronological investigation of this species has been conducted in the US to corroborate reports of longer-lived *Ailanthus* in the US. Nevertheless, large *Ailanthus* trees throughout the eastern US have been reported that far exceed the previously established maximum 107 cm DBH (Fig. 2; Illick and Brouse 1926), from which some of the earliest age estimations for *Ailanthus* were inferred.

Research objectives

The goal of our project was to elucidate where *Ailanthus* occurs, where long-established individuals and populations persist, and what factors have initiated recent widespread invasion throughout PA forests. We had two main objectives: 1) determine feasibility of using *Ailanthus* tree-ring chronologies to aid in reconstruction of tree and stand/site histories throughout the Northeast, determine the maximum age of *Ailanthus*, and explore age/diameter relationships for historical inference and temporal reconstruction; and 2) evaluate county-level incidences of extant *Ailanthus* populations throughout PA with emphasis along highway corridors, in urban and suburban epicenters where historic populations of *Ailanthus* are well documented, and within forests where recent *Ailanthus* invasions have been reported. Using these data along with historic records and accounts, an up-to-date spatiotemporal timeline for *Ailanthus* range expansion throughout PA from the earliest points of introduction forward to recent invasions of forest lands was generated.

Methods

Study area

The Mid-Atlantic region of the eastern US including Delaware (DE), Maryland (MD), NJ, PA, Virginia (VA), and West Virginia (WV) along with the eastern edge of the Midwest region (Indiana [IN], Ohio [OH]) and the northern edge of the Southeast region (Kentucky [KY], Tennessee [TN]), supports the highest densities of *Ailanthus* in the US (Invasive Plant Atlas of the US, http://www.invasiveplantatlas.org/). Since *Ailanthus* was first introduced into PA almost 230 years ago, this region may support numerous large and presumably old *Ailanthus* trees from which life history patterns can be obtained using tree-ring chronologies. The main tree-ring study herein includes *Ailanthus* trees from DE, NY, OH, PA, VA, and WV with emphasis on SE PA (Fig. 4). Within SE PA, trees were sampled within, or adjacent to, points of early introduction, including trees from the Woodlands Cemetery where *Ailanthus* was first introduced in ca. 1784, Bartram's garden where an *Ailanthus* sucker from Hamilton's tree was planted in 1809, and from Pratt's Garden (Lemon Hill Mansion) where *Ailanthus* was planted in the first decades of the 19th century (Fig. 2, Appendix 2). The *Ailanthus* study area includes all counties in PA and builds on previously characterized populations (McWilliams et al. 2007, Rhoads and Klein 1993, Wherry et al. 1979). A second tree-ring study was implemented to determine when *Ailanthus* first invaded state forest lands; this study included *Ailanthus* of various ages and sizes (Fig. 4).

Dendrochronology

Tree Core Data. To locate the largest *Ailanthus* trees throughout the study area, we utilized State Big Tree Registry reports (Hill 1986, Wade 2006), online databases (e.g., http://www.pabigtrees.com/), and referrals from state registry coordinators and measurements crews, state foresters, arboretum staff, arborists, and state and city park invasive species specialists. We also established contacts with grounds managers at private estates throughout SE PA where large *Ailanthus* had been observed. Letters were mailed to private residences to obtain permission to sample large candidate trees.

A minimum of one radial core was extracted from each *Ailanthus* tree using a 76-cm, 5.15-mm diameter Haglof increment borer (Haglof Inc., Madison, MS). If internal rot was detected during core extraction, a second, and occasionally a third, increment core was taken if permission was granted by the owner. All cores, including those with internal rot, were transferred to pre-labeled straws for drying and processing. *Ailanthus* leaf tissue was also collected from trees with foliage for genetic analyses as part of a peripheral study.

Increment cores were prepared as described by Stokes and Smiley (1996) and Swetnam et al. (1985). Cores were air-dried inside straws for 3–5 days, glued into routed wooden blocks, and taped to secure cores for 2–5 days of additional drying. Intact cores were sanded with an orbital palm sander using 100- and 220-grit sandpaper. Cores were further sanded by hand using a series of sandpapers to 2400-grit, followed by polishing with lamb's wool to remove fine particulate matter and enhance the wood surface for microscopic examination and ring measurement.

Ring-width measurements (0.01 mm) were conducted using a Velmex sliding stage micrometer (Velmex Inc., Bloomfield, NY). Marker years (excessively narrow or wide annual rings) were recorded. Using marker years, individual tree

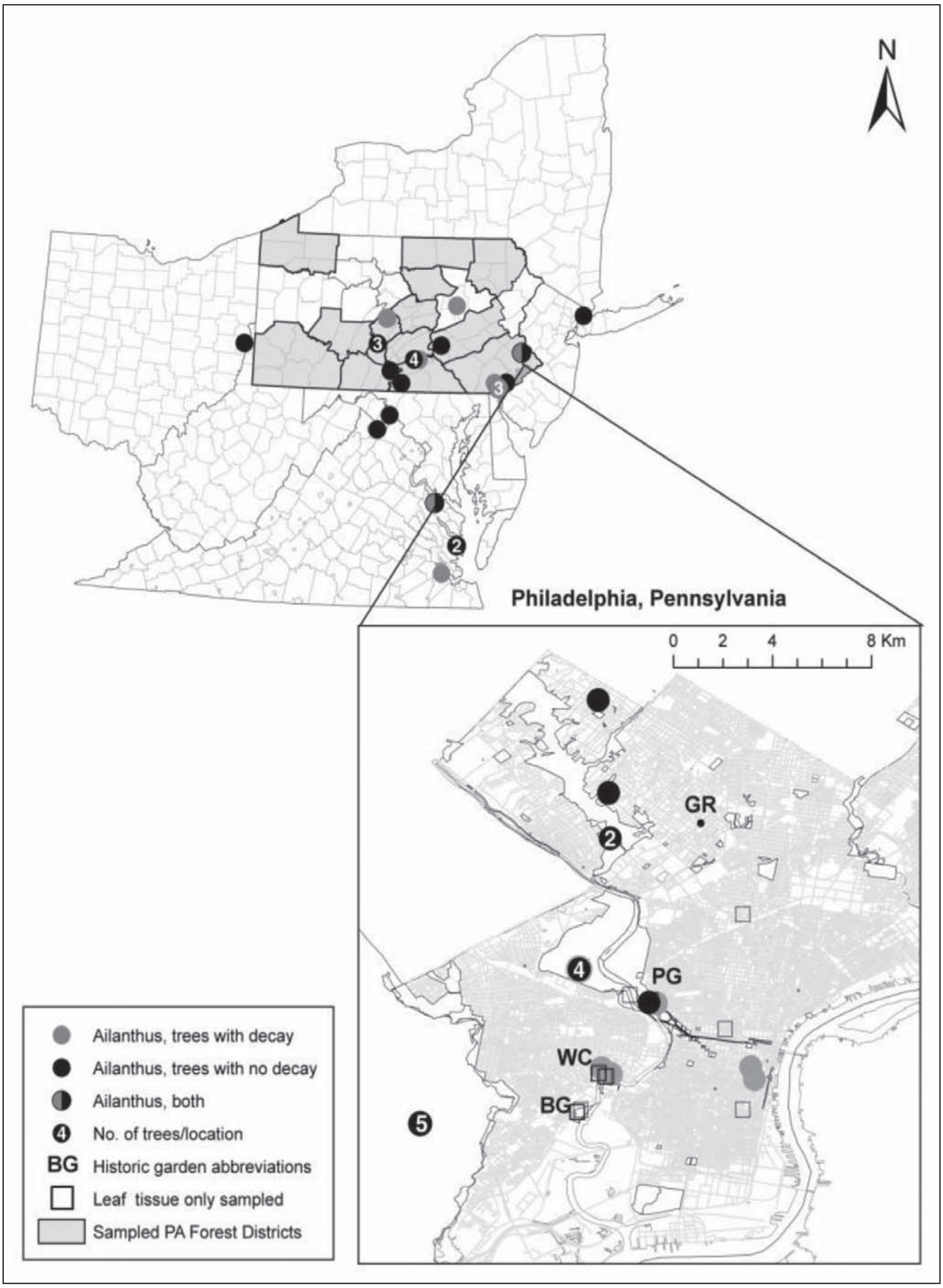

Figure 4. Map of study area including detail of Philadelphia, PA, where most trees in the large tree study were sampled. Filled circles without numbers indicate only one tree cored at that given location. Historic garden abbreviations are as follows: BG = Bartram's Garden, WC = Woodlands Cemetery (formerly The Woodlands), PG = Pratt's Garden (Lemon Hill), and GR = Grumblethorpe. Highlighted DCNR forest districts (filled gray areas) indicate where *Ailanthus* were sampled on state and federal forest lands. Counties sampled in state-wide survey not included (see Fig. 13).

chronologies were adjusted as needed by inserting locally absent ring values or subtracting false rings (Holmes 1983, Yamaguchi 1991). A minimum core segment length of 50 years was used for cross-dating older trees. For younger *Ailanthus* trees previously sampled by Schall (2008) on the PA Tuscarora State Forest, a segment length of 30 years was used; these cores were analyzed separately because of their young age. Following initial visual cross-dating, ring-width series for all cores were evaluated using the quality-control program COFECHA (Holmes 1983), a statistical program that calculates series inter-correlations and identifies segments that exhibit cross-dating problems within individual series. Problematic cores that could not be accurately dated were discarded.

Growth responses and patterns in Ailanthus. *Ailanthus* tree-rings are classified as ring porous with distinct boundaries, a characteristic ideal for tree-ring research (Fritts 1976, Rawlings and Staidl 1924). However, little is known concerning *Ailanthus*' radial growth patterns, propensity for ring anomalies such as false and missing rings, or sensitivity to high-frequency variations in annual growth. In addition, dioecious tree species such as *Ailanthus* have shown differential responses in radial growth to climate and exogenous stress, depending on plant sex (Cedro and Iszkuło 2011, Gao et al. 2010, Iszkuło and Boratyński 2011), emphasizing the need to compare growth patterns between male and female *Ailanthus* trees. This difference is particularly important since *Ailanthus* females are prolific seed producers, capable of producing >300,000 seeds/tree annually for sustained periods of time (Bory and Clair-Maczulajtys 1980) and a maximum of a million seeds annually for larger female *Ailanthus* trees (Illick and Brouse 1926). Such extensive seed production is a sink for carbohydrates and likely impacts stem growth as compared to non-seed-producing (e.g., male) counterparts.

We conducted an investigation of *Ailanthus* throughout PA and surrounding areas, in which we compared annual tree-ring patterns to detect common annual growth signals among *Ailanthus* trees. All growth series were cross-dated using COFECHA with the previously described methodology. Master chronologies were compared to individual chronologies to assess the strength of common growth signals. Mean sensitivity and mean inter-series correlations were evaluated. Mean sensitivity is a measure of the relative change in ring-width from one year to the next in a given series, whereas inter-series correlation is a measure of the strength of the signal common to all sampled trees at the site.

Age prediction for *Ailanthus*

To predict ages of large *Ailanthus* trees with internal rot, which precluded total age measurements, as well as historically documented individuals, we utilized two approaches. First, we explored age-diameter relationships using linear regression analysis, which allowed us to predict total age at DBH, despite internal rot and missing annual rings near the tree center, by using DBH. However, preliminary analyses revealed the method applicable only to open-grown, single-stem trees. Nevertheless, this method proved very useful for predicting year of planting/establishment for open-grown historic *Ailanthus* trees, using only the diameter measurements as reported in 19th- and 20th-century publications, which was subsequently used to help validate historic first reports as well as establish if areas of earliest cultivation were also areas of sustained colonization.

Ailanthus trees were assigned to one of three site-class categories: 1) open-grown: a tree with no competition, 2) forest co-dominant: tree with both inter- and intra-specific competition, and 3) cohort-grown: open-grown group of *Ailanthus* with intra-specific competition only from individuals within the same cohort. Initial regression analysis revealed no correlation between diameter and age for forest co-dominants, which were then excluded from regression analysis. The remaining *Ailanthus* trees were further classified as either single or multi-stemmed. Multi-stemmed individuals included low forking (below DBH) stems, as well as multi-trunk trees that had fused. Multi-stemmed individuals were also excluded from analysis after initial regression output revealed no correlation between diameter and age for this group of trees. In addition, trees >140 cm DBH were excluded from this analysis, since data points from these large trees fell outside the predictable range for which age could be accurately estimated.

The second analysis utilized mean ring widths and core measurements to estimate the number of rings in partial cores, where the innermost rings were missing due to rot. A preliminary analysis of 13 complete cores, representing trees from 30–130 cm DBH, revealed that a minimum of 35% of the core was needed to predict age ± 20 years ≈70% of the time (Appendix 3). Preliminary analysis indicated that this method could be used across all site-class categories, as well as single- or multi-stem trees. If usable core length was 75% of the total core length, age ± 10 years could be predicted 77% of the time (Appendix 3). Using a 95% intact core, age ± 6 years could be predicted 100% of the time with exact predictions 30% of the time (Appendix 3). Extant trees were included regardless of site and stem class, unlike the regression analysis. This analysis was then used on extant trees with partial tree cores. Age estimates were calculated by projecting the mean ring width of the partial core across the length of the missing core segment and adding this estimated ring count to the existing ring count.

Ailanthus floristic surveys

Historic surveys and reports: To establish where *Ailanthus* had been previously known to occur in PA, we conducted an exhaustive query of all known literature and searchable databases to establish a base map from which migration patterns could be hypothesized.

County-level surveys. Historically, surveys to determine geographic distribution of flora in PA relied mainly on herbarium specimens (Rhoads and Klein 1993, Wherry et al. 1979). Although this type of survey can accurately determine a plant species' extant distribution at the time of sapling, it cannot reveal if a species persists over time at a given location. Persistence is especially important in geographic regions where only a few individuals represent the entire population. As a means of circumventing these problems, our study included a county-level survey in which specimens were collected from at least one location within every county where extant *Ailanthus* occurred. Leaf tissue from male and female

Ailanthus and, depending on timing of sampling and availability, mature seed from female trees was collected from 2010–2011 for use in peripheral studies.

Forest surveys and site history reconstruction. Although *Ailanthus* was first introduced into PA in ca. 1784, casual observations by foresters suggest this species has only recently become widespread within public forests. To resolve when *Ailanthus* first invaded these forests, as well as determine the stand history, we conducted a tree-ring study within a number of state and federally managed lands, including one state game preserve, two state parks, seven state forests, the Allegheny National Forest, and US Army Corps of Engineers lands with confirmed *Ailanthus* populations.

At each location, the largest *Ailanthus* tree, as well as three or four adjacent *Ailanthus* trees, representative of average-sized stems within the stand, were either felled, from which a cross-section disk was removed at stump level, or sampled at DBH with an increment borer. Our preliminary studies revealed no significant difference between age at stump height and age at DBH. Determination of tree age and growth patterns allowed us to determine probable year when most *Ailanthus* invaded each site. In addition, it allowed us to determine if *Ailanthus* had been present in the stand prior to the last major site disturbance, such as timber harvesting, or conversely, if the species invaded the site after the disturbance. *Ailanthus* stem cross-sections from one location on the PA Tuscarora State Forest that had been previously collected for another study (Schall 2008) were also utilized to add robustness to the dataset. All cross-section and core samples were air-dried and prepared for tree-ring counting as described previously.

Results

Tree-ring data

Seventy-five increment cores were extracted from 26 large *Ailanthus* trees, as well as from 24 additional *Ailanthus* trees growing across numerous historic locations and sites of interest (Fig. 4). Of these 50 trees, 37 trees were from PA, six from VA, four from DE, and one tree each from OH, NY, and WV (Table 1).

Growth and internal decay. Diameters of the 50 *Ailanthus* trees ranged from 39.1–197.4 cm DBH with an average diameter of 86.1 cm (Table 1). Trees included the overall PA State Champion (HSAa10; Fig. 5A) as defined by the PA Forestry Association and the National Champion (HSAa09; Fig. 5C) as defined by American Forests, National Register of Big Trees.

Internal decay (heartwood rot), resulting in partial increment cores, occurred in 16 of 50 (32%) of the old *Ailanthus*, and averaged 44% decay/tree (% missing wood from extracted core[s]) with a range of 4–89% decay for all *Ailanthus* containing internal rot (Table 1). Average DBH for trees with detectable internal decay was 106.6 cm compared to 76.5 cm for trees without detectable decay (Table 1). Amount of internal rot within individual *Ailanthus* trees appeared to be symmetric around the circumference, although a few rotten *Ailanthus* trees had successive cores that varied by as much as 40% in total length, which justified extraction of multiple cores from some rotten trees, especially when mean

Table 1. Sampling date, location, size, condition, age, and genetic relationships for *Ailanthus* trees sampled in the Northeast US.

Tree ID[A]	Year sampled	General location	Site class[B]	Plant gender[C]	Stem class[D]	DBH (cm)[E]	Heart rot (%)	No. rings	Age[F]
HSAa01[1]	2010	Longwood Gardens, Kennett Square, PA	2	A	1	88.1	38	64	?/101
HSAa02[1]	2010	Woodlands Cemetery, Philadelphia, PA	1	A	2	116.1	73	32	100/?
HSAa03[1]	2010	Woodlands Cemetery, Philadelphia, PA	1	A	1	102.6	5	80	88/82
HSAa04	2010	Private residence, Lansdowne, PA	2	A	1	72.1	-	83	83
HSAa05[1]	2011	Private residence, Lansdowne, PA	2	A	1	51.3	-	92	92
HSAa06[1]	2011	Private residence, Lansdowne, PA	2	A	1	61.2	-	97	97
HSAa07[1]	2010	Private residence, Lansdowne, PA	2	A	1	70.1	-	80	80
HSAa08[2]	2010	New York Botanical Gardens, Bronx, NY	1	G	1	85.9	-	79	79
HSAa09	2010	Montross Inn, Montross, VA	1	A	1	197.4	89	37	?/?
HSAa10	2010	Aldie Mansion, Doylestown, PA	1	A	2	144.0	39	74	?/96
HSAa11[1,2]	2010	Chestnut Hill Community Center, Chestnut Hill, Philadelphia, PA	1	A	1	132.6	-	117	117
HSAa12[1]	2010	Private residence, Society Hill, Philadelphia, PA	1	A	1	129.0	75	22	112/?
HSAa13[2]	2010	Dickinson College, Carlisle, PA	1	A	1	100.6	-	80	80
HSAa14[2]	2010	Dickinson College, Carlisle, PA	1	A	1	103.9	-	85	85
HSAa15[2]	2010	Dickinson College, Carlisle, PA	1	A	1	87.9	-	84	84
HSAa16[2]	2010	Dickinson College, Carlisle, PA	1	A	1	93.2	-	79	79
HSAa17	2010	Dickinson College, Carlisle, PA	1	A	1	103.6	62	33	88/85
HSAa18[1]	2010	Sisters of St. Francis of Philadelphia, Red Hill Farm, Aston, PA	2	A	1	71.1	-	57	57
HSAa19[2]	2010	Aldie Mansion, Doylestown, PA	1	A	1	80.0	-	42	42
HSAa20	2010	Raystown Lake, Huntingdon, PA	2		1	39.9	-	48	48
HSAa21	2011	Montross Inn, Montross, VA	1	G	2	87.9	-	60	60
HSAa22	2010	Michaux State Forest, Mont Alto, PA	2	U	1	66.0	-	62	62
HSAa23[2]	2010	Pennsylvania State University, University Park, PA	1	G	1	112.8	13	86	97/97*
HSAa24[2]	2010	Fairmont Park, Shofuso Japanese House, Philadelphia, PA	3	A	1	76.5	-	58	58
HSAa25[2]	2010	Fairmont Park, Shofuso Japanese House, Philadelphia, PA	3	A	1	53.3	-	42	42
HSAa26[1,2]	2010	Fairmont Park, Walnut Lane Golf Course	3	A	1	58.4	-	76	76

Table 1, continued.

Tree ID^{A}	Year sampled	General location	Site class^{B}	Plant gender^{C}	Stem class^{D}	DBH (cm)^{E}	Heart rot (%)	No. rings	Age^{F}
HSAa27^{1,2}	2010	Fairmont Park, Walnut Lane Golf Course	3	A	1	62.0	-	77	77
HSAa28^{1}	2010	Fairmont Park, W. Sedgewick Street	2	A	1	74.4	-	61	61
HSAa29^{2}	2010	Fairmont Park, Lemon Hill Mansion	1	A	1	108.5	-	107	107
HSAa30	2010	Fairmont Park, intersection of Sedgeley and Kelly Drive	2	G	1	65.3	34	78	?/96
HSAa31	2010	Fairmont Park, Shofuso Japanese House	3	A	1	56.1	25	58	44/77
HSAa32^{1,2}	2010	Fairmont Park, Shofuso Japanese House	3	A	1	50.0	-	59	59
HSAa33^{2}	2010	Fairmont Park, Shofuso Japanese House	1	A	1	69.9	-	55	55
HSAa34	2010	Bloomsburg Hospital, Bloomsburg, PA	1	G	2	68.8	4	64	56/64
HSAa35^{2}	2010	Raystown Lake	3	A	1	39.1	-	47	47
HSAa36	2010	Raystown Lake	2	A	1	43.2	-	41	41
HSAa37	2010	Buchanan State Forest, Franklin County, PA	2	A	1	37.6	-	17	17
HSAa38	2011	Broken Rock Road, Bakerton, WV	2	A	1	98.3	-	79	79
HSAa39	2011	Wilmington Country Club, Wilmington, DE	3	A	1	107.7	79	14	93/?
HSAa40	2011	Wilmington Country Club, Wilmington, DE	3	A	1	92.5	21	73	78/90
HSAa41	2011	Wilmington Country Club, Wilmington, DE	3	A	2	89.9	37	63	76/80
HSAa42^{2}	2011	Wilmington Country Club, Wilmington, DE	3	A	1	59.4	-	34	34
HSAa43	2011	Private residence, Foster, VA	3	D	2	134.1	-	98	98
HSAa44^{2}	2011	Private residence, Foster, VA	3	A	1	85.6	-	96	96
HSAa45	2011	Private residence, Smithfield, VA		A	2	127.8	58	67	111/111
HSAa46	2011	Rosemont Manor, Berryville, VA	1	A	2	126.5	-	64	64
HSAa47^{1}	2011	Private residence, Lansdowne, PA	2	A	1	131.6	-	105	105
HSAa48	2011	Independence National Historical Park, Indepdence Square, Philadelphia, PA	1	A	1	103.1	49	40	88/75
HSAa49	2010	Fernwood State Forest, Jefferson County, OH	2	U	1	50.8	-	60	60
HSAa50*	2011	State Game Lands #211, Dauphin, PA	2	G	1	39.6	-	41	41
HSAa51*	2011	Bartram's Garden, Philadelphia, PA	-	U	-	-	-	-	-

Table 1, continued.

Tree ID[A]	Year sampled	General location	Site class[B]	Plant gender[C]	Stem class[D]	DBH (cm)[E]	Heart rot (%)	No. rings	Age[F]
HSAa52*	2011	Bartram's Garden, Philadelphia, PA	-	U	-	-	-	-	-
HSAa53*	2011	Bartram's Garden, Philadelphia, PA	-	U	-	-	-	-	-
HSAa54*	2011	Bartram's Garden, Philadelphia, PA	-	U	-	-	-	-	-
HSAa55*	2011	Bartram's Garden, Philadelphia, PA	-	U	-	-	-	-	-
HSAa56*	2011	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa57*	2011	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa58*	2011	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa59*	2011	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa60*	2010	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa61*	2010	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa62*	2010	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa63*	2010	Woodlands Cemetery	-	U	-	-	-	-	-
HSAa64*	2011	Fairmont Park, Lemon Hill Mansion	-	U	-	-	-	-	-
HSAa65*	2011	Fairmont Park, Lemon Hill Mansion	-	U	-	-	-	-	-
HSAa66*	2011	Fairmont Park, Lemon Hill Mansion	-	U	-	-	-	-	-

[A] Tree IDs followed by a number 1 indicate trees that were cross-dated and used to develop a master chronology for *Ailanthus* in southeastern PA. Trees followed by a number 2 indicate *Ailanthus* trees used in regression analysis. Trees HSAa50–61(*) were seedlings or saplings not included in the tree-ring analysis but were part of the floristic studies and were cataloged in the DNA library for peripheral studies.

[B] Site class refers to environment in which trees were found 1 = open-grown, 2 = forest co-dominant, and 3 = cohort-grown. Dash indicates no data.

[C] *Ailanthus* is androecious (A) or gynoecious (G). Trees of unknown status (U) and dead trees (D) are marked accordingly.

[D] Stem class refers to trees as either 1 = single-stemmed or 2 = multi-stemmed but having a single stem at breast height .

[E] Diameter at breast height (1.4 m above soil line).

[F] Age estimates for trees lacking pith or curvature. The first age estimate is based on linear regression, and the second age estimate is a projection of mean ring width (See methods for details).

Figure 5. Examples of large extant *Ailanthus* included in this study A) HSAa10, Aldie Mansion, Doylestown, PA State Champion *Ailanthus*, The Pennsylvania Forestry Association; B) HSAa29, Lemon Hill, Philadelphia; C) HSAa09, Montross, VA, National Champion *Ailanthus*, American Forests, National Register of Big Trees; and D) HSAa23, The Pennsylvania State University, University Park, PA. B and D are the two oldest seed-producing *Ailanthus* in the US, to our knowledge. Photos taken by M.T. Kasson and L.R. Kasson.

ring width was used for age prediction (data not shown). Regression analysis of percentage internal decay versus DBH revealed a significant positive linear relationship (% internal decay = 0.494[DBH] - 8.8; $R^2 = 0.391$, $P = .01$). However, DBH accounted for only ≈40% of variability in percentage decay, indicating that other factors contributed to predicting internal decay.

Age distribution of intact Ailanthus. Ages for *Ailanthus* trees, confirmed by ring counts to pith, ranged from 17–118 yrs with a mean of 76 yrs (Table 1). Three trees from PA were >100 years old, including the oldest individual in the study (HSAa11 in Chestnut Hill, Philadelphia), which was 119 years old in 2012 (Figs. 6, 7). To our knowledge, this is the oldest *Ailanthus* reported within the US or abroad where age determination was supported with tree-ring data. Despite our determinations of advanced age in extant *Ailanthus*, no individuals exceeded 120 years in age, and therefore could not be directly linked with documented 1st-generation plantings or establish direct evidence to corroborate ties among early historic planting locations. Nevertheless, the older-aged cohort in and around Philadelphia likely represents naturalized populations established from seed or sprouts of late 18th-century or early 19th-century plantings. However, genetic studies are needed to resolve such relationships. Average age was noticeably less for forest- and cohort-grown *Ailanthus* (66 and 65 yrs, respectively) compared to open-grown *Ailanthus* (80 yrs) (Table 1).

Seed-producing Ailanthus. Six out of 50 large *Ailanthus* trees were females, as indicated by presence of seed clusters. Females averaged 76.7 cm DBH as compared to 87.4 for male or sexually *ambiguous Ailanthus* (Table 1). Two of the sexually reproducing females, including a 107-year-old female tree at Lemon Hill Mansion in Fairmont Park, Philadelphia, and a 97-year-old female tree at The Pennsylvania State University, University Park, represented the oldest seed-producing female *Ailanthus* trees reported to our knowledge (Fig. 5B, D). As of 2012, seed from the latter *Ailanthus* tree was viable (M. Kasson, pers. observ.).

Growth responses and patterns in *Ailanthus*

General growth characteristics. Annual raw ring width ranged from 0.49–17.14 mm across all sampled *Ailanthus*, with a mean annual ring width of 4.23 mm. Rings within the first 10 years of intact cores were excluded from measurements (but not age determinations), since the large rings normally produced in juvenile wood are not normally measured in dendrochronological studies unless first fit to a negative exponential curve (Fritts et al. 1969). Trees from VA and WV had larger average annual ring widths of 5.12 mm, compared to average ring widths of 4.39 mm from PA and NY.

The SE PA region chronology possessed relatively strong common signals within the greater Philadelphia area and southeastern PA but not beyond. The SE PA chronology consisted of 15 *Ailanthus* sampled across 10 geographically distinct locations separated by a maximum distance of 68 km (Table 1, Fig. 8A). Annual raw ring width for these trees ranged from 0.49–17.14 mm with a mean annual ring width of 4.02 mm. Common signals were reflected in the significant inter-series correlation value of 0.350, greater than the critical correlation

Figure 6. Photographs of the oldest *Ailanthus* tree (see arrow) in this study (Aa11, 119 years old in 2012). Photographs show the same tree in 1918 (top) and 2011 (bottom). Tree was 132.6 cm DBH at time of core extraction in 2010. Tree is immediately adjacent to Chestnut Hill Community Centre, 8419 Germantown Avenue, Philadelphia, PA. 1918 photo reprinted with permission of the Chestnut Hill Historical Society. Most recent photo (2011) taken by M.T. Kasson.

coefficient of 0.3281 for the 99% confidence level, using a 50-year segment length. Mean sensitivity was 0.303 (range = 0.145–0.409), a value considered acceptable for tree-ring dating (Grissino-Mayer 2001). *Ailanthus* trees HSAa29, HSAa30, and HSAa33, all seed-bearing female trees, were excluded from the chronology. Preliminary analysis of increment cores from these individuals revealed that including cores from female *Ailanthus* significantly weakened inter-series correlations in the SE PA chronology, and their growth was negatively correlated with the master chronology (Fig. 8B). Additionally, a suspected clone of four *Ailanthus* trees in Fairmont park (HSAa24, HSAa25, HSAa31, and

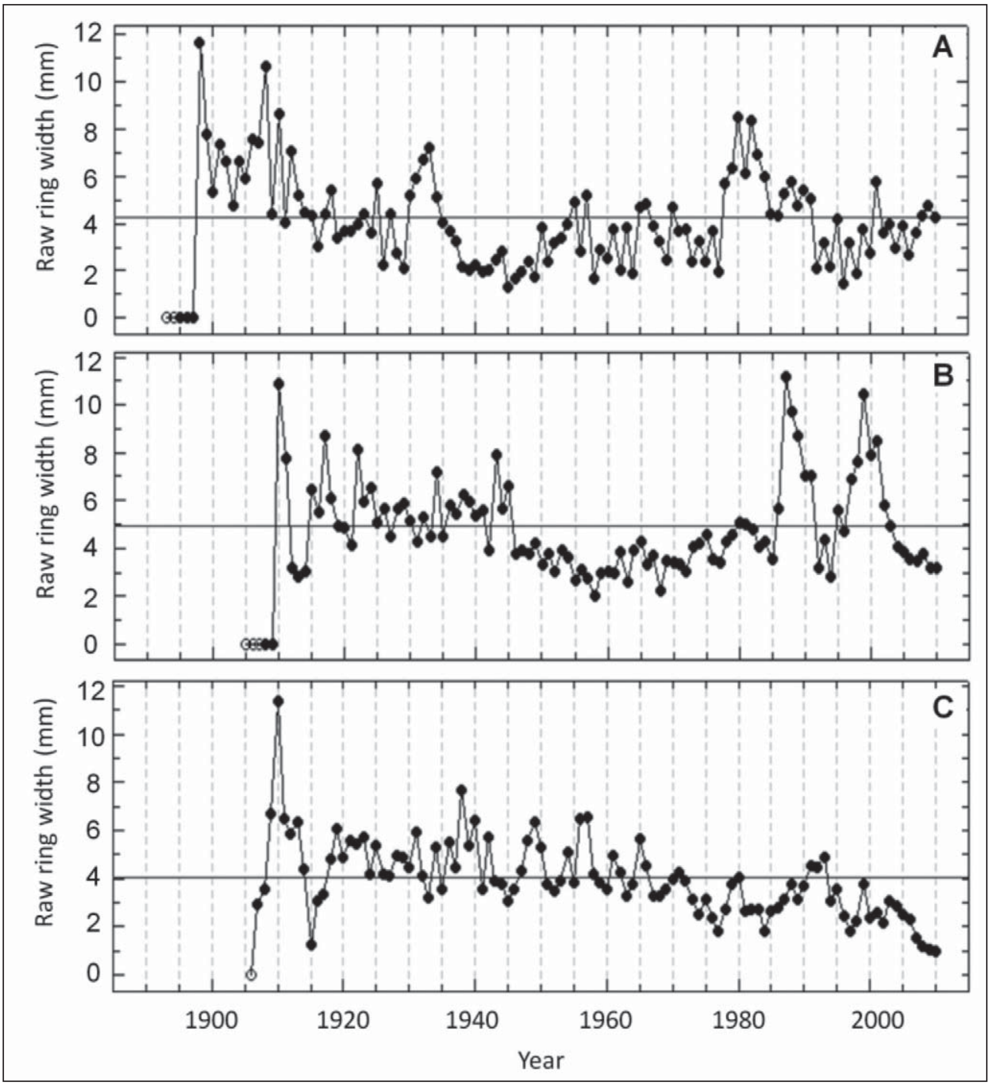

Figure 7. Raw ring width chronologies of the oldest individual *Ailanthus* trees in this study: A) HSAa11, B) HSAa29, and C) HSAa47. Horizontal line denotes the average ring width for each chronology. Zero values at the far left of each chronology indicate either actual rings that were not measured (filled circles) or estimated rings (hollow circles) based on pith estimators for trees with curved innermost annual rings, but lacking pith.

HSAa32), and two other *Ailanthus* (HSAa19 [Aldie] and HSAa04 [Lansdowne]) were removed due to negative correlation values despite confirmation of the highest correlation predicted by COFECHA.

A separate master chronology was developed from 22 *Ailanthus* trees sampled from a large forested stand, which had established following *Lymantria dispar dispar* L. (Gypsy Moth) salvage logging in 1983 on the PA Tuscarora State Forest (Schall 2008). This master chronology possessed strong common signals resulting in an inter-series correlation value of 0.540 and mean sensitivity of 0.417 (Fig. 8b). A majority of *Ailanthus* trees in this stand were ultimately killed by the soil-borne vascular wilt pathogen, *Verticillium nonalfalfae* Inderb. et al. (formerly *V. albo-atrum* Reinke and Berthold*)*, which also caused a steady decline in radial growth after 2000 (Fig. 8b; Schall 2008, Schall and Davis 2009a).

Cross-dating of *Ailanthus* chronologies from three geographically separated areas within the primary tree-ring study revealed considerable variability in growth patterns. PA sites included Dickinson College (five *Ailanthus* trees) and Lansdowne (four trees excluding HSAa05), and a private residence in Foster, VA

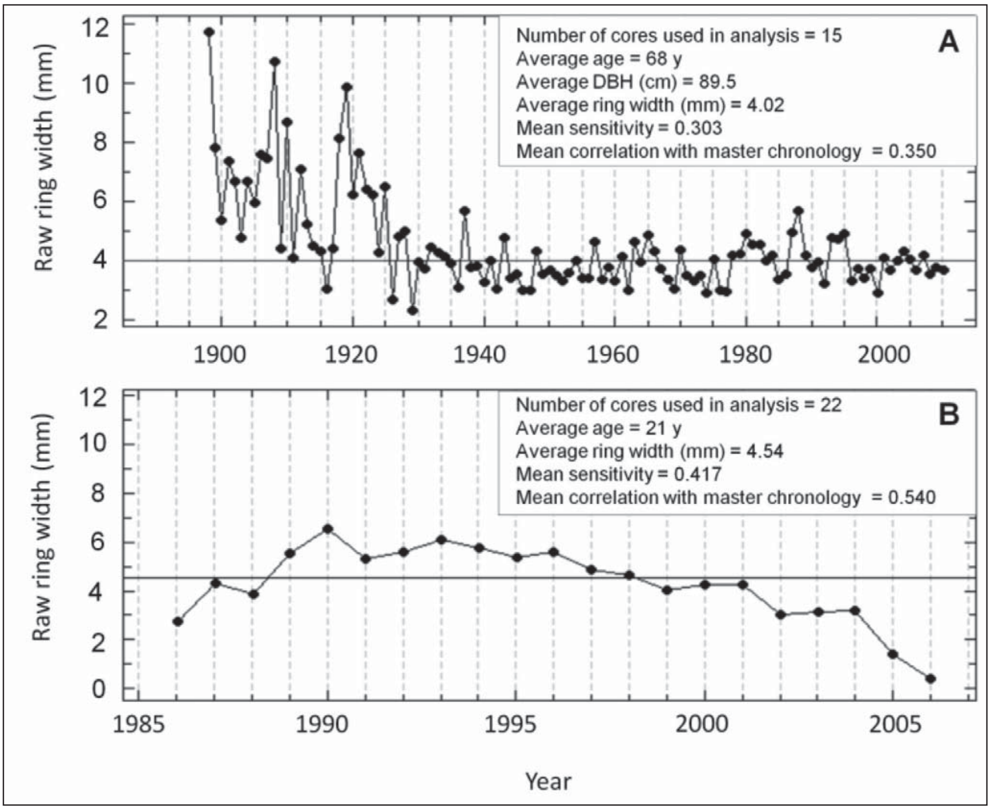

Figure 8. Raw ring-width master chronologies of *Ailanthus* trees: A) 15 large *Ailanthus* throughout southeastern PA, and B) 22 dead and dying *Ailanthus* naturally infected with *Verticillium nonalfalfae* in the PA Tuscarora State Forest (Schall and Davis 2009a). Horizontal line denotes the average ring width for each chronology. COFECHA output values are provided in the upper right hand corner for each master chronology.

(two trees). The four *Ailanthus* trees at Lansdowne shared strong common signals, resulting in an inter-series correlation value of 0.411 and an average mean sensitivity of 0.311. Five *Ailanthus* trees at Dickinson College lacked common signals across all segments despite being separated by only <100 m. Although mean sensitivity was 0.368, increment core patterns appeared decoupled from ambient conditions, possibly indicating stand-level variability unrelated to climate. In VA, two trees, identical in age, shared common signals with inter-series correlation value of 0.437 and mean sensitivity of 0.307 yet had diameters that varied by almost 50 cm DBH. This finding again indicates that other external factors were contributing to growth differences.

Growth and annual ring anomalies. Although *Ailanthus* cores are ring porous with obvious tree-ring boundaries, false rings occurred in 30 of 100 examined *Ailanthus*, including 18 of the 50 large *Ailanthus* trees and averaged 3.57 false rings/tree (range = 1–15 false rings/tree) for a total of 107 false rings (Table 1). False rings appeared as a dark single row of gum-filled cells (Fig. 9). Although location of false rings within a given growth ring varied, the majority usually occurred near the middle of the annual ring. False rings occasionally occurred adjacent to early wood vessels (Fig. 9D), but were difficult to distinguish in this location (Fig. 9). For seven trees, >2 false rings occurred within the same calendar year on one or more occasions (Fig. 9A, D). Only six trees exhibited false rings in the same year, but common false rings did not occur in trees from the same geographic region, or at the same location within a specific annual ring. Conversely, several rotten trees had multiple partial cores containing false rings, some within the same calendar years and intra-ring locations for two or three cores taken >90° apart, indicating that the false rings likely extended around the entire circumference.

More than 90% of the false rings occurred within annual growth rings formed after 1980 (Appendix 4). However, due to significant internal rot near the center of some trees, incidence of false rings could not be determined before 1980 in three of the largest, hollow *Ailanthus* trees (17%; Appendix 4). Furthermore, a number of false rings may not have been detected because they were not present within the increment core sample.

To identify a possible cause of false rings in *Ailanthus*, we examined trees that had been previously inoculated with a native vascular wilt fungus, *Verticillium dahliae* Kleb. (Schall and Davis 2009a). This pathogen is known to produce vascular discoloration and induce occlusion in the xylem, without killing infected trees, which could result in false rings. False rings were found present in *Ailanthus* trees that had been inoculated with *V. dahliae*, but not in all increment core samples (Fig. 9c). However, stem cross-sections from felled *Ailanthus* that had been inoculated with *V. dahliae* exhibited false rings in 100% of the excised cross sections, and only in growth rings that developed after inoculation. We also examined *Ailanthus* trees that were naturally infected with *V. dahliae* in a related unpublished study. Some cross-sections from felled trees, as well as some increment cores, contained false rings and yellow discoloration, an internal symptom associated with *Verticillium* infection (Fig. 9D). The false rings were discontinuous around the tree circumference, which explains the lack of false rings in some increment cores, since the core represents a small percent of the total cross section.

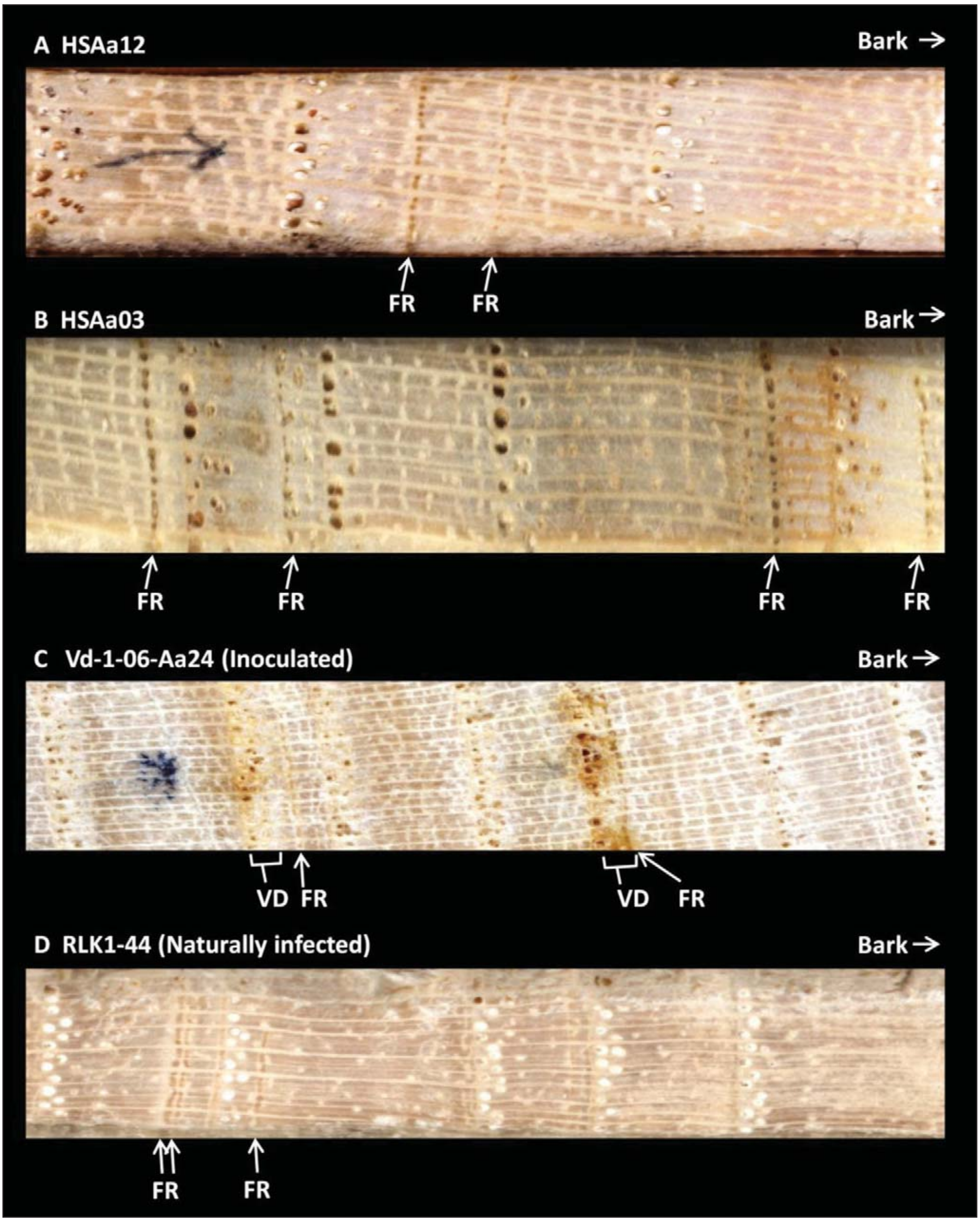

Figure 9. Annual growth ring boundaries and false rings (FR) in *Ailanthus* increment cores. False rings are shown as dark tangential bands (white arrows) within the annual growth ring boundaries and include: A). HSAa12, Chestnut Hill, Philadelphia; B) HSAa03, The Woodlands, Philadelphia; C) Vd-1-06-Aa24, a 2006 *Verticillium dahliae* inoculated *Ailanthus* from a previous study (Schall and Davis 2009a); and D) RLK1-11-Aa21, a naturally-occurring *V. dahliae*-infected *Ailanthus*. VD denotes vascular discoloration preceding the FR within the same annual growth ring.

Other radial growth anomalies were also revealed from this study. In particular, the chronology from HSAa05, growing near Philadelphia, showed an unusual alternating pattern of narrow/wide annual radial growth from 1927–1965 (Fig. 10). No false rings were apparent in these cores, nor was this pattern detected in adjacent similarly aged *Ailanthus* trees (Table 1). This tree also exhibited below average growth during 1968–2010 (Fig. 10). The cause of this anomaly is unknown.

Differential growth responses in male vs. female Ailanthus. Preliminary cross-dating using COFECHA revealed low inter-series correlations values for female *Ailanthus* as compared to the SE PA master chronology. In addition, inter-series correlation values among seed-producing females were not significant. On the contrary, an attempt to cross-date female trees from the same location, such as HSAa29 and HSAa30, revealed no common signals between the trees, resulting in negative inter-series correlation values. Expanding the chronology to include female *Ailanthus* outside SE PA further weakened this relationship.

Age prediction for *Ailanthus*

Regression analysis revealed a highly significant positive linear relationship ($R^2 = 0.795$, $P = 0.0001$) between *Ailanthus* DBH and age (Fig. 11). This relationship held for large, intact trees as well as from reputable historic observations (trees with reported diameters and accompanying photographs and/or descriptions) within PA (Fig. 11). *Ailanthus* trees included in the regression analysis are

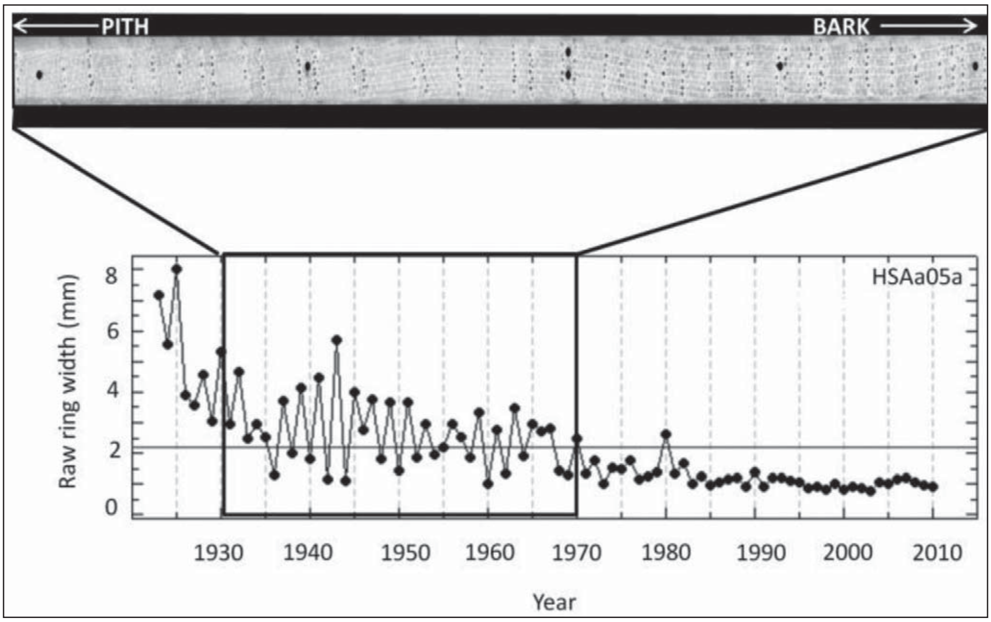

Figure 10. Radial growth anomalies in *Ailanthus*. Tree HSAa05, Lansdowne, PA, showed an unusual alternating pattern of narrow-and-wide annual growth rings from 1927–1965. Single dots on the core indicate decadal marks while double dots indicate the half-century mark. No false rings were apparent nor were these patterns detected in four other large *Ailanthus* in close proximity and included in this study. In addition, this tree exhibited below average growth from 1968–2010.

listed in Table 1. Diameter accounted for nearly 80% of all variability in age for open- and cohort-grown, single-stemmed *Ailanthus*. Using this regression equation, ages and associated year of origin were estimated for extant, decayed (e.g., hollow) trees (Table 1), as well as previously reported large trees for which only DBH measurements existed (Table 2). Predicted ages for extant *Ailanthus* ranged from 44–112 years, with the oldest individuals occurring within Philadelphia (112 and 100 years) and southern VA (111 years) (Table 1). These age estimations based on DBH corroborate ages derived from extant, intact *Ailanthus*. Regression analysis provided age estimates for HSAa02, HSAa12, and HSAa39, which could not be predicted using mean-ring width analysis since the percentage decay exceeded our acceptable limit. For historic trees where diameter measurements were taken directly from published reports, predicted ages ranged from 48–120 years (Table 2). These estimations revealed initial establishment of *Ailanthus* in six PA counties 70–118 years earlier than previously reported. Furthermore, predicted ages in combination with extant tree-ring data confirmed nearly continuous colonization of *Ailanthus* at Bartram's Garden, Philadelphia spanning two centuries and a century or more at several other locations throughout Philadelphia and SE PA including Lemon Hill Mansion, Woodlands Cemetery, and Chestnut Hill (Fig. 12).

Although all *Ailanthus* trees fell within the range of diameters from which accurate age predictions could be made, stem-class could not be determined for many historic trees. This uncertainty may have resulted in over-estimations of age (Table 2), even though multi-stemmed trees represented a relatively small proportion (16%) of the overall extant study population (Table 1). However,

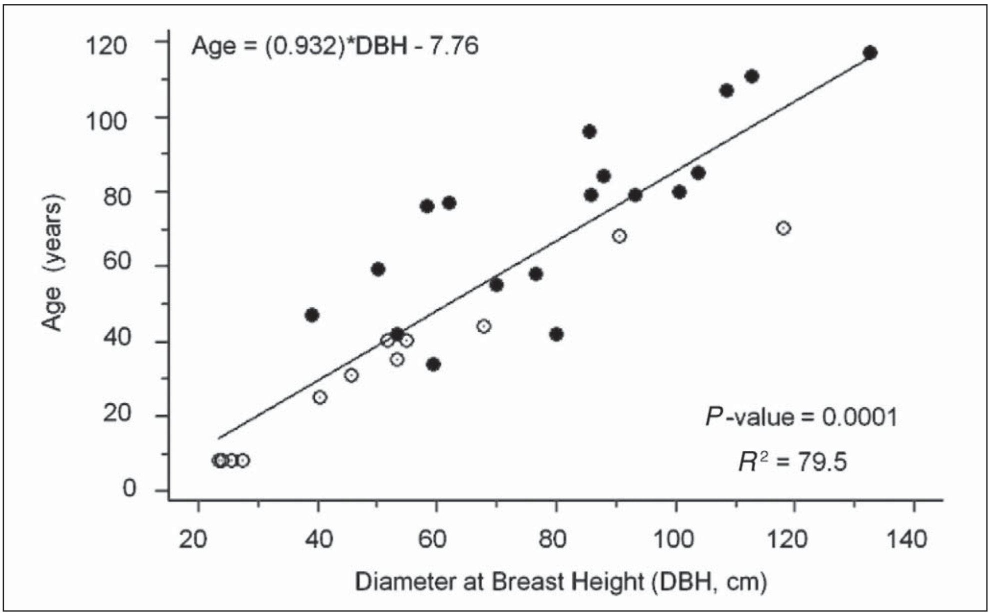

Figure 11. Relationship between age and DBH of open-grown, single-stem *Ailanthus* trees sampled throughout Pennsylvania from 1835–2011. Filled circles denote trees cored for this study during 2010–2011, whereas unfilled circles denote historical observations found in various publications from 1835–1950 (see Appendix 2 for historical observations references).

Table 2. Estimated ages and year of introduction for historic *Ailanthus* trees in Pennsylvania using linear regression. Date = date of measurement[A]. Age = estimated age in years. Year = year of introduction.

Tree location	Date	DBH (cm)	Age	Year	References
Bartram's Garden, Philadelphia	1853	67.8	55	1798	Meehan 1853
	1877	90.7	77	1800	Sargent 1878
Humphrey Marshall's Arboretum, Marshallton (Chester County)	1893	60.0	48	1845	Sargent 1893
Grumblethorpe, Philadelphia	1904	118.1	102	1802	Jellett 1904
Bartram's Garden, Philadelphia	1919	71.7	59	1860	Anonymous 1919
River Front Park, Harrisburg (Dauphin County)	1924	83.8	70	1854	Phillips 1924
Carlisle (Cumberalnd County)	1925	76.2	63	1862	Illick and Brouse 1926
Five Forks (Franklin County)	1925	103.6	89	1836	Illick and Brouse 1926
Mooredale (Cumberland County)	1925	106.7	92	1833	Illick and Brouse 1926
	1925	97.5	83	1842	Illick and Brouse 1926
	1925	97.5	83	1842	Illick and Brouse 1926
	1925	85.3	72	1853	Illick and Brouse 1926
	1925	82.3	69	1856	Illick and Brouse 1926
Pine Grove Furnace (Cumberland County)	1925	91.4	77	1848	Illick and Brouse 1926
Waynesboro (Franklin County)	1925	97.5	83	1842	Illick and Brouse 1926
Private Residence, York Springs (Adams County)	1925	91.4	77	1848	Illick and Brouse 1926
Marshall's Arboretum, Marshallton (Chester County)	1925	61.0	49	1876	Illick and Brouse 1926
	1925	76.2	63	1862	Illick and Brouse 1926
Lutheran Theological Seminary, Gettysburg (Adams County)	1925*	81.8[B]	68	1857	LutheranTheologicalSeminary,Gettysburg,PAPhotoArchives
	1925*	61.0[B]	49	1876	LutheranTheologicalSeminary,Gettysburg,PAPhotoArchives
	1925*	61.0[B]	49	1876	LutheranTheologicalSeminary,Gettysburg,PAPhotoArchives
Bartram's Garden, Philadelphia	1937	106.7	92	1845	Anonymous 1937
Private Residence., Harrisburg (Dauphin County)	1968	122.2	106	1862	Mickalitis 1969
Private Residence, Steelton (Dauphin County)	1978	127.0	111	1867	Hill 1986
Lebanon Valley Engraving, Lebanon (Lebanon County)	1988**	126.2	110	1878	Clark 1988
Awbury Arboretum, Philadelphia (Philadelphia County)	1988	136.7	120	1868	Clark 1988
Private Residence, Tunkhannock (Wyoming County)	1990	137.4	120	1870	Clark 1991

[A] Date of measurement sometimes preceed year of publication by several years; therefore, year of publication was used to provide the most conservative estimate of age possible. * denotes estimates from photographs taken between 1911–1925. ** indicates the *Ailanthus* reported in Lebanon County had a year of most recent measurement in 1900 but appears to be a gross error given this observation was published in 1988.

[B] Measurements were estimated from old photographs and based on current measurements of architectural features (see Fig. 3A).

having multiple *Ailanthus* observations within some counties increases the likelihood that at least one of these trees/county were single-stemmed, resulting in a more accurate estimation of year or decade of establishment (Table 2). In addition, old photographs from some locations also confirmed that many historic *Ailanthus* trees were single-stemmed (Fig. 3).

Mean ring-width analysis, the second analysis used in this study, accurately predicted ages for only extant *Ailanthus,* with a range of 80–111 years. Ages of two trees were within 5 years of regression estimations, and age of one tree was identical to the regression prediction (Table 1). Mean ring-width analysis provided age estimates for *Ailanthus* trees HSAa01, HSAa10, and HSAa30, which could not be predicted using linear regression since these individuals did not meet regression site class and/or stem-class criteria (Table 1). In general, mean ring analysis tended to over-estimate age for intact *Ailanthus* cores compared to regression analysis, but predictions were more accurate for trees <79 cm DBH (Appendix 3). For trees >79 cm DBH, mean ring width predictions were less accurate, except for trees with <25% internal decay (Appendix 3). Furthermore, this over-estimation of age in intact trees increased dramatically as modeled percent internal decay increased. Given the average percentage internal decay for trees with partial cores, emphasis should be placed on regression values rather than ring-width estimations if decay exceeds 25% (Table 1, Appendix 3).

Ailanthus Floristic Surveys

Historic surveys and reports: Previous literature yielded numerous observations of Ailanthus incidence from its introduction forward to the initiation of

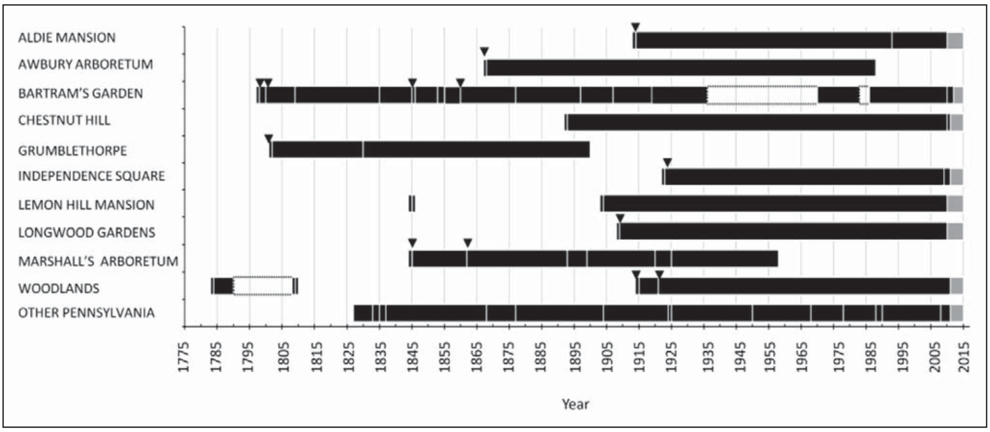

Figure 12. Historical accounts of *Ailanthus* trees found throughout PA from time of introduction through 2012. Vertical white lines represent documented *Ailanthus* observations. Filled bars (black) denote time periods with confirmed *Ailanthus* colonization, whereas hashed lines denote time periods without reported observations but with high probability of occurrence. Black triangles denote estimations of establishment and/or planting date based on either linear regression or mean ring-width estimates. Gray bars indicate likelihood of survival beyond publication of the monograph. Other Pennsylvania locations denote both historic and non-historic locations and include observations across ten PA counties (see Appendix 2 for complete list of references).

this study in 2010 (Appendix 1, 2). Incidence of *Ailanthus* increased noticeably between 1820 and 1855, from two extreme SE PA counties to 10 counties forming several geographically distinct populations of *Ailanthus* throughout the state (Fig. 13). By 1925, many of the scattered geographic pockets of *Ailanthus*

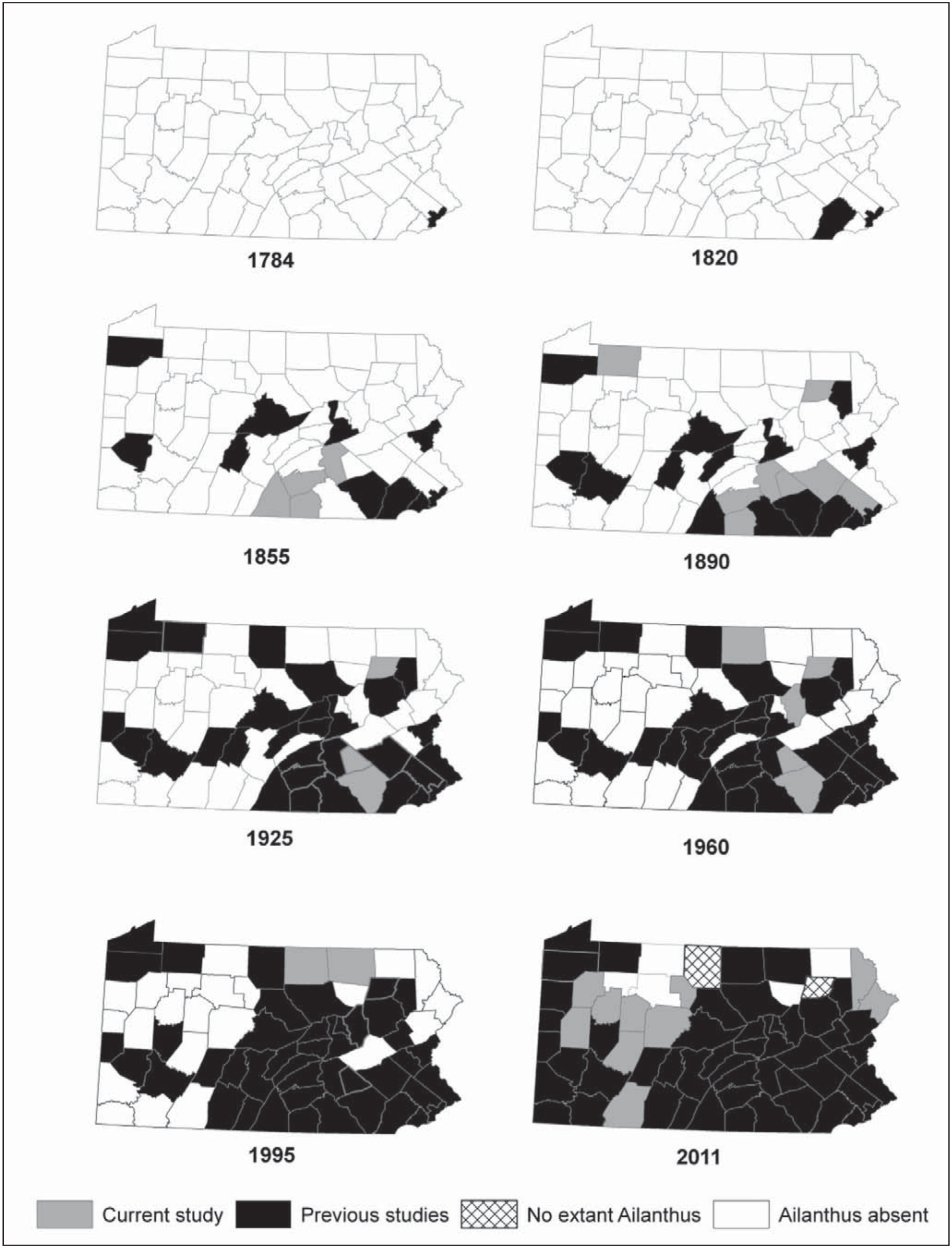

Figure 13. Amended first reports of *Ailanthus* in PA (1784–2011) by county based on historic accounts, herbarium specimens, recent observations, and dendrochronology. Cross-hatch counties in the 2010 map signify no recent confirmation of *Ailanthus* since earlier published reports. See Tables 1 and 2 for amendments.

had coalesced, adding 17 new counties to the species' geographic range in PA (Fig. 13). The majority of new counties were in the southern half of the state, where expanded railroad routes formed continuous corridors and likely played a role in *Ailanthus* seed dissemination.

Between 1960 and 2010, reports of *Ailanthus* in western PA increased noticeably, with the addition of 11 new counties to its range, as well as the addition of six new counties in northeastern PA to its range (Fig. 13). As of 2010, *Ailanthus* had been reported in 51 of 67 PA counties. Based on previous reports, *Ailanthus* was largely absent from the northwestern and northeastern regions of PA, likely due, in part, to hard freezes and minimal forest fragmentation or soil disturbance which impeded *Ailanthus* colonization and expansion (Croxton 1939).

County-level field surveys: A total of 135 samples were collected from 60 of the 67 PA counties (Table 1, Appendix 5). Our sampling resulted in first reports of *Ailanthus* in nine PA counties: Butler, Cameron, Clarion, Clearfield, Columbia, Pike, Somerset, Venango, and Wayne. *Ailanthus* had not been reported from these counties in previous inventories or surveys (Fig. 14) (McWilliams et al. 2007, Rhoads and Klein 1993, Wherry et al. 1979). Our surveys also revealed that *Ailanthus,* previously reported in Potter and Wyoming counties within the northern tier of PA, are no longer present and have not been observed since these early reports (Fig. 13).

In addition to tissue samples for a DNA library, increment cores were also extracted from *Ailanthus* trees in Tioga and Bradford counties where *Ailanthus* had not been reported in previous flora surveys, but was listed after 2004 in FIA inventory data (McWilliams et al. 2007). Tree-ring studies confirmed that *Ailanthus* had been growing in these two counties for 50 and 35 years, respectively. In both locations, seed-producing females represented the oldest individuals.

Trees and saplings along roadways and near urban centers represented >70% of all *Ailanthus* sampled in PA (Appendix 5), which supports similar findings in WV where *Ailanthus* distribution was correlated with more urbanized counties (Huebner 2003). Evaluation of several forested areas adjacent to the sampled areas revealed no *Ailanthus* populations (data not shown), emphasizing the propensity of the species for open disturbed areas.

State forest surveys: A total of 38 *Ailanthus* stands were confirmed across two federally managed forested areas, four state parks, ten state forests, four state game lands, and Fairmont Park in Philadelphia (Fig. 14). Seventeen stands were selected for tree-ring analysis that represented a wide range of *Ailanthus* ages, densities, management histories, ownerships, and geographic locations (Table 3). Additional *Ailanthus* stands that contained *Ailanthus* were identified in the Delaware Water Gap (Eichelberger and Perles 2009), but were not surveyed by the authors.

Maximum age of *Ailanthus* trees in the surveyed stands ranged from 12–91 years across all locations, with a mean age of 36 years (Fig. 14a). Age, incidence, and mean diameter of *Ailanthus* generally decreased as latitude increased (Fig. 14, Table 3). As expected, trees near Philadelphia were

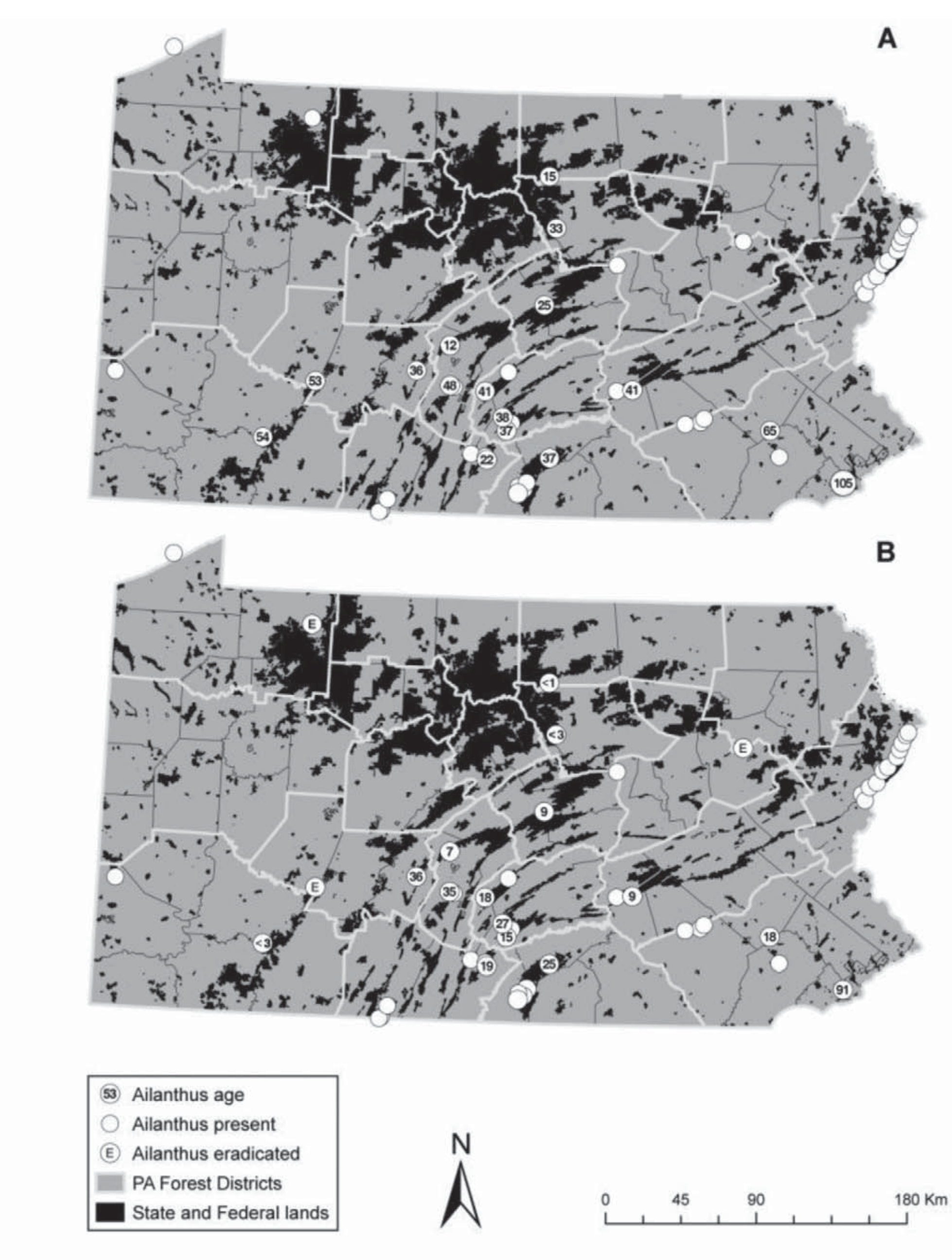

Figure 14. Incidence of *Ailanthus* on PA state and federal lands by forest district, 2010–2011. Numbers indicate (A) maximum age (living or recently killed) and (B) mean age of living *Ailanthus* at each location. See Table 2 for stem densities and ages, stand history, and management history and status. Circles in Delaware County, PA (lower right corner) denote *Ailanthus* trees on private land (HSAa04-07, 47) that were used as proxy due to scarcity of state forest lands near Philadelphia. However, *Ailanthus* from Fairmont Park (HSAa29) were similar in age to trees at Lansdowne and are reflective of maximum ages in this region (Table 1).

Table 3. Location, stand history, and current management stratagies for *Ailanthus* on PA and federal forests. DBH = average diameter at breast height in cm. Age = max/mean[A].

			Ailanthus				
State forest district, county/ General Location	Stand history/details	Most recent disturbance	Year of origin	No. trees present	DBH	Age	Year of intervention/ strategy[B]
Bald Eagle, Centre BESF, Lickhollow Road Tract	Timber harvest between 1966–68.	1968	1960s	2500–5000	8	14/9	2003, H-P
Gallitzin, Blair Canoe Creek State Park, Water Tower Road Tract	Former farm lands acquired between 1960s–1970s.	1970s	1974	1000–2500	18	36/36	2009, BC-SC
Buchannan, Franklin BSF, Tobacco Road, Letterkenny Tract	32-ha clearcut, following 70% mortality from a multi-year Gypsy Moth infestation.	1988	1989	5000–10,000	18	22/19	2008, BC-SC
Cornplanter, Warren Allegheny National Forest, Warren	Natural gas well site (shallow well) immediately adjacent to *Ailanthus*.	Unknown	2009	1—10	<3 cm	1/E	2010, H-E
Gallitzin, Indiana GSF, Clark Run Natural Area, Cramer	Invasion near edge of parking lot along Rt. 403, north of Johnstown.	Unknown	1957	10—25	<3 cm	53/33	2007, H-E
Rothrock, Huntingdon Army Corps of Engineers, Raystown Lake, Orchard Road Tract	29-ha clearcut from harvested *Pinus virginiana*.	1960s	1960	2500–5000	13	51/35	2008, BC-SC
Michaux, Cumberland MSF, Bunker Hill Road Tract	40-ha clearcut, Oak Leafroller defoliation.	1966	1974	5000–10,000	18	37/25	2008, BC-SC
Tiadaghton, Lycoming TSF, Pine Creek Rail Trail, Waterville	Female *Ailanthus* planted in 1930s at Camp Kline arboretum ajacent to abandoned railroad.	2007	1973	50–100	4	33/3	2007, H-P
Tioga, Tioga TSF, Pine Creek Rail Trail, Blackwell	53-year-old female *Ailanthus* adjacent to river and abandoned railroad (tree removed 2010).	Unknown	1995	<20	< 1 cm	15/1	2010, H-P
Weiser, Dauphin State Game Lands #211, Wild Turkey Timber Tract	18-ha clearcut, timber sale. Bridge built in 1996 followed by roads in 1997.	1999	1970	2500–5000	7	41/9	2008, BC-SC

Table 3, continued.

State forest district, county/ General Location	Stand history/details	Most recent disturbance	*Ailanthus* Year of origin	No. trees present	DBH	Age	Year of intervention/ strategy[B]
William Penn, Berks French Creek State Park, Elverson	Roadside invasion.	Unknown	1917, 1987	<50	25	95/24	None, none
Forbes, Westmoreland Donegal Township, Tabernacle Road Tract	Herbicide killed *Ailanthus*.	2008	1957	<50	<5 cm	54/3	2008, H-P
Rothrock, Huntingdon Mule Road	3-ha selction cut adjacent to 14-ha clearcut in 1971.	1971	1999	<50	8	12./7	None, None
Tuscarora, Franklin and Perry TSF, Second Narrows Road Tract	54-ha. salvage harvest of dead oak trees following Gypsy Moth defoliation.	1983	1962	10,000	18	49/25	2000, BC-SC
Tuscarora, Mifflin TSF, Sugar Valley Tract	Timber sales by DCNR in 1962–1964 (selection harvest), 1978, 1997–1998 (TSI), and 2001 (salvage shelterwood).	1997	1971	< 250	13	13/40	2009, BC-SC
Tuscarora, Franklin TSF, Burns Valley Tract, Franklin County	1963: first road in this valley built for timber sale. Timber sales by DCNR in 1963–1964 (selection harvest) and 1986 (Gypsy Moth salvage).	1986	1970	1000–2500	23	41/28	2006, BC-P
Tuscarora, Franklin TSF, Blue Mountain Tract	1970–1973: first road in this valley built for timber sale. Gypsy Moth defoliation chronic from 1982–1989. Understory dominated by Striped Maple and prospects for desirable regeneration were poor. 1988-1990: salvage clearcut of the area.	1989–1990	1971	>10,000	21	37/19	2006, BC-SC

[A] Maximum age includes both living and recently killed trees, whereas mean age is based on age of surviving cohort.

[B] Management strategies are as follows H = herbicide, BC = biological control (see Schall and Davis 2009a, b), P = persistent (incomplete control by herbicide), SC = sustained control, and E = eradicated. None indicates stands where no control measures have been implemented as of 2011.

noticeably older than trees further west and north. At nine separate forest sampling locations, thousands of *Ailanthus* trees formed continuous single-aged stands indicative of widespread invasion following a large disturbance (Table 3). However, in other stands, older scattered *Ailanthus* trees had existed years before the last major timber harvest or natural disturbance. Seed from female trees in these stands likely accounted for later invasion of *Ailanthus* in disturbed sites (Table 3). Salvage logging of oak-dominated hardwood stands, in the aftermath of extensive Gypsy Moth and *Archips semiferanus* Walker (Oak Leaf-roller)-induced mortality, permitted unprecedented invasion by *Ailanthus* at four of these locations (Table 3). Other invasions onto state and federal lands resulted from plantings on private residences, adjacent to or on state forest property, where seed was likely disseminated outward from the original planting locations. In addition, PA has leased in-holdings of land on state forests, primarily for hunting camps, for more than a century. Some camps have plantings of exotic tree species for ornamental purposes and/or feeding wildlife. Seed from large seed-bearing *Ailanthus* trees at some of these camps have led to establishment of *Ailanthus* within nearby state forests and other public lands (Table 3). These secondary populations now are capable of invading additional state forest lands following future disturbances.

Discussion

Feasibility of using *Ailanthus* in tree-ring studies

Age and radial growth response. Prior to this study, no thorough evaluation had been conducted to determine the life span of *Ailanthus* and if *Ailanthus* trees could be successfully used in cross-dated tree-ring studies. Here we report that *Ailanthus* reaches ages up to 119 years, which supports a previous report of a 117-year old *Ailanthus* in England (Cutler et al. 1993) as well as anecdotal evidence of long-lived *Ailanthus* in PA (Wentz 1950). Greater than 20% of the large *Ailanthus* cored had, or were estimated to have, 95 or more annual growth rings, especially in urban and suburban environments where life expectancy might actually be enhanced due to limited competition and reduced exposure to pathogens common in forest soils. Therefore, we conclude that *Ailanthus* can routinely live to >100 years of age. However, concentration of oldest individuals in fragmented urban environments coupled with a high incidence of internal decay may have discouraged previous investigations, resulting in the misconception that *Ailanthus* trees were short-lived. Illick and Brouse (1926) reported that heartwood rot was most prevalent in *Ailanthus* trees >90 cm DBH and increased rapidly with diameter, which is consistent with our observations. However, large intact *Ailanthus* trees were found in high enough frequency to encourage further investigation of this species' age structure as well as potential for tree-ring analyses. Large trees are still common throughout early points of introduction, including the Philadelphia area, New York City, and Narragansett Bay, RI. The age of large *Ailanthus* trees in these areas might surpass the maximum life expectancy of *Ailanthus* determined herein, and may offer additional insight into the maximum life expectancy and growth patterns of this species. A review of Champion

Tree Registries in other states as well as historic literature, suggests that large old *Ailanthus* trees may exist elsewhere.

Regarding cross-dating, Schall (2008) conducted a preliminary tree-ring study in which he cross-dated a single local cohort of *Ailanthus*, but did not report COFECHA values. Although there is no standard minimum number of annual growth rings required for successful cross-dating, the reliability of cross-dating often diminishes rapidly for series <40 years in length, and tree-ring chronologies from short-lived species should be treated with caution (Cook and Kairiūkštis 1990). Furthermore, rapidly growing, shade-intolerant species such as *Ailanthus* often contain numerous growth rings within the juvenile wood. Juvenile wood is the youngest wood near the pith, is strongly influenced by competition, and differs anatomically from mature wood. These factors complicate inclusion of juvenile wood in tree-ring analyses (Worbes 2002). Therefore, previous reports that *Ailanthus* was short-lived (e.g., 50 years) coupled with its juvenile growth characteristics, may have precluded its consideration for tree-ring analysis.

Strong common signals ideal for tree-ring studies were found among old *Ailanthus* trees within a 68-km radius of Philadelphia, but not beyond. In addition, *Ailanthus* comprising a single younger cohort of trees within the PA Tuscarora State Forest cross-dated very well despite their young age, suggesting that reliability of cross-dating *Ailanthus* may occur even at young ages in some stands. Inter-series correlations were statistically significant within both groups, indicating that diameter growth of *Ailanthus* trees within each of the two locations was responding similarly to exogenous factors such as climate. Successful cross-dating of sub-groups of large *Ailanthus* within this greater Philadelphia area also revealed strong common diameter growth signals within geographically delimited clusters. In contrast, several *Ailanthus* trees at Dickinson College separated by <100 m lacked common signals, suggesting that either site-specific factors or growth complacency, due to exogenous factors (e.g., fertilization, supplemental watering), likely accounted for the lack of common growth signals. Similar trends were observed in a suspected clone of *Ailanthus* trees at the Shofuso Japanese House in Fairmont Park where three of four trees growing within 3 m and far removed from other *Ailanthus* trees lacked common signals, could not be cross-dated, and therefore were not included in the master chronology.

Ripple and Larsen (2000) and Larsen and Ripple (2003) reported that cross-dating among *Populus tremuloides* Michx. (Trembling Aspen) trees was unsuccessful in clonal stands in northern Yellowstone National Park. They reported that vegetative propagation and intra-specific root grafting not only helps maintain discrete aspen populations but may also explain unsuccessful cross-dating among individual trees within a given population. Intra-specific root grafting likely occurs within *Ailanthus* clones as well (Kowarik 1995). Jelínková et al. (2009) reported substantial interconnectivity within trembling aspen clones via interclonal grafts, which may contribute to growth complacency among individual stems. Similarly, Fraser et al. (2006) observed that less competitive trees gained resources from adjacent trees through root grafts, although the overall impacts of grafts were less evident on aboveground responses such as annual growth rings. Nonetheless, the authors stated that even a moderate transfer of resources to a subordinate tree could reduce competitive asymmetry in grafted trees, especially when resource transfer occurs year after year. Root graft studies with Trembling Aspen, *Pinus banksiana* Lamb. (Jack Pine), and *Pinus contorta* Douglas (Lodgepole Pine) reported that age of trees at time of graft initiation varied considerably from 2–90 years, as does time required to complete the graft and duration of the graft (Fraser et al. 2005, Jelínková et al. 2009, Tarroux and DesRochers 2010). These findings involving several species suggest that the influence of intraspecific grafts on individual trees varies in time and space. Despite the potential for growth complacency among *Ailanthus* at individual sites, *Ailanthus* trees from the Tuscarora State Forest shared strong common signals. It is likely that these trees seeded into the site following large scale logging, as compared to arising vegetatively from the root systems of harvested parent *Ailanthus* trees. Such findings indicate that incremental growth sensitivity in *Ailanthus* may be a proxy indicator for the absence and/or reduced incidence of root grafts. However, studies are needed to test this hypothesis.

Growth characteristics and anomalies. Observations of >140 stem cross sections and increment cores collected across the northeastern US confirmed *Ailanthus* to be ring porous with obvious annual ring boundaries. However, false rings with obvious gum deposits occurred in >20% of trees examined and >40% of large trees cored for age determination, and were especially common within the older trees in the greater Philadelphia area (Appendix 4).

Gum deposits and tyloses are common features in vessels and tracheids that have ceased to function, and have been associated with false-ring formation in diseased trees (Christiansen et al. 1999, Ragazzi et al. 2002). In *Ailanthus excelsa* Roxb. (Indian Tree-of-Heaven), vascular occlusions (gum deposits) develop in response to infection by fungi (Shah and Babu 1986), which supports our observations. Ragazzi et al. (2002) showed that declining *Quercus robur* L. (English Oak) exhibited gum deposits and false rings from which *Fusarium solani* f. sp. *eumartii* (Carpenter) Snyder and Hanson was consistently isolated. Although our results revealed false annual rings within large *Ailanthus* trees infected with *V. dahliae*, it is unclear why the incidence of false rings increased dramatically among large non-inoculated *Ailanthus* after 1980, particularly throughout SE PA (Appendix 4).

Unprecedented dieback and mortality of *Ailanthus* by *V. dahliae* was reported after 1995 in CT, NY, and VA (Emmerich et al. 1998), which might indicate a change in conditions after 1990 ultimately favored attack of *Ailanthus* trees by *V. dahliae*. One plausible explanation for these results might be related to tree age at time of false ring formation. Although false rings were observed during the first 50 years of growth of a few *Ailanthus*, the majority of false rings occurred in *Ailanthus* tree-rings formed after >60 years of age. Older trees may be more predisposed to agents such as *V. dahliae* that may cause such ring anomalies. Otherwise, factors influencing radial growth anomalies were likely due to changing climate phenomena or other abiotic factors beginning in the early 1980s, after which a majority of false rings were formed. Alternatively, trees with ring anomalies may represent remaining survivors of a larger *Ailanthus* population that succumbed to disease from the 1980s–1990s, when Verticillium wilt was observed across the region.

Although Verticillium wilt provides a unifying explanation as to the cause of false rings in *Ailanthus*, it does not explain why the incidence of false ring formation increased after 1980. One plausible explanation for this temporal pattern is the inadvertent introduction of an exotic ambrosia beetle from Asia, *Euwallacea validus* Eichhoff (formerly *Xyleborus validus*) (Curculionidae: Scolytinae), which was first detected in the US in NY in 1976 and SE PA (Delaware County) in 1980 (Wood 1977, 1980). Although *E. validus* has a wide host range in its native China and East Asia, this beetle primarily attacks stressed, dying, or recently dead *Ailanthus* trees in the US (Schall 2008). Preliminary studies by Schall (2008) and our own studies (M.T. Kasson, M.D. Davis, and D.D. Davis, unpubl. data) revealed that this beetle can passively disseminate *Verticillium* fungi, which offers an explanation of how previously uninfected stressed trees may have become infected in recent decades.

Other growth anomalies (e.g., the alternating pattern of narrow/wide radial growth in HSAa05) were not as widely observed as false rings, suggesting other localized or genetic-mediated phenomena associated with these anomalies.

Age prediction. Regression analysis of open- and cohort-grown, single-stemmed *Ailanthus* trees revealed a highly significant positive linear relationship between tree diameter and age of intact living trees, as well as ages estimated from diameters taken from reputable historic observations. These analyses support the age/diameter regression curves for aging historic trees as well as rotten extant trees. However, some caveats apply when using this approach. First, extending the diameter-age relationship to large individuals that fall outside the modeled range is not recommended. Exceptionally large diameter trees may represent statistical outliers; therefore, using simple linear regression results in over-estimation of age of these large trees. Paradoxically, these trees often contain the most significant internal rot and/or may be hollow, precluding accurate age measurements, as was the case for HSAa09, the US National Champion *Ailanthus*.

Secondly, it is unrealistic to assume that diameter-age relationships constructed from data collected among *Ailanthus* trees in the Northeast would accurately describe the relationship for *Ailanthus* growing at other locations. Further, age and diameter may not be closely related in some areas, due to competition among individual trees, as well as differing biotic and abiotic stresses, all of which may cause marked differences in growth rates (Cook and Kairiūkštis 1990). Such differences can be observed in even-aged stands having a wide variation of diameters (Cook and Kairiūkštis 1990). For example, within the Buchanan State Forest in south-central PA (location of HSAa37), we observed that a single cohort of 22-year-old *Ailanthus* trees had diameters ranging from 10–38 cm DBH. Similarly, Espenschied-Reilly and Runkle (2008) reported DBH ranges of >26 cm for 20–25-year-old *Ailanthus* within a woodlot in Ohio. Such variability in diameter emphasizes the importance of including categorical variables such as stem-class and crown-class within regression models, thus reducing the magnitude of errors.

Mean ring-width analysis, the second method used in this study, accurately predicted ages for extant *Ailanthus* with some overlap in age predictions based on regression analysis (Table 1). Because mean ring-width analysis tended to over-estimate age for intact (non-rotten) *Ailanthus* cores compared to regression analysis, it is uncertain to what degree pre-existing decay, especially significant levels of decay (e.g., >70% heart rot), affects current ring formation and average growth rates. However, when applied to *Ailanthus* with <25% decay or in combination with regression analysis in order to make direct comparisons of predicted ages, mean ring width analysis provides a simple and useful analysis for estimating age in *Ailanthus* trees with internal decay.

From cultivation to widespread invasion: A spatiotemporal timeline for *Ailanthus*

Ailanthus has been present in PA for nearly 230 years, a residency time second among invasive tree species only to *Acer platinoides* L. (Norway Maple), present within the state since ca. 1756 (Rhoads and Block 2002). However, *Ailanthus* has presumably surpassed Norway Maple with regard to invasiveness, fragmenting and disrupting entire native ecosystems. Despite a long residence history, early *Ailanthus* introductions may not represent the initiation of a sustained, expanding invasion despite continuous colonization in some urban locations such as Bartram's Garden. On the contrary, sustained widespread invasion by *Ailanthus* apparently did not occur until the mid- to late 20th century (Fig. 13, Table 3).

To better understand this contradiction, and the implications for management of forest stands that contain the invasive *Ailanthus*, we must consider the invasion strategy and history of *Ailanthus*. *Ailanthus* cultivation and widespread planting did not gain significant momentum until after 1820, when the species became commercially available as an ornamental tree in the eastern US. At the same time, seed-producing (pistillate) *Ailanthus* trees were first observed, after which the first major expansion of *Ailanthus* within its naturalized range occurred, likely related to seed production and resultant seedlings (Fig. 14). Similarly, Hamilton's first-reported introductions (ca. 1784) of staminate Lombardy Poplar and *Broussonetia papyrifera* (L.) Vent. (Paper Mulberry), required a second introduction of pistillate plants to allow seed production and subsequent spread of seedlings (Browne 1846, Downing 1851, Swearingen 2005).

Further expansion of the naturalized range of *Ailanthus* did not intensify in western PA until after 1890, when widespread expansion of railroad systems presumably fostered invasions of weedy invaders such as *Ailanthus*. For example, the famous railroad Horseshoe Curve near Altoona, PA, was completed by the Pennsylvania Railroad in 1854, effectively traversing the steep Allegheny Mountains and connecting Philadelphia and Pittsburgh. However, widening of the curve to support four tracks did not occur until 1898, after which the volume of train traffic across PA increased dramatically. Concurrently, the incidence of *Ailanthus* in counties through which main railroad corridors passed also increased. Secondary spread (e.g., expansion from founding foci) of *Ailanthus* in PA was likely facilitated via colonization of railway embankments. The colonization of the open railway corridors, in combination with wind turbulence generated by passing trains, allowed for widespread dissemination of *Ailanthus* seed and subsequent colonization by seedlings, which is common among other weedy and invasive species (Conolly 1977, Gelbard and Belnap 2003, Harrison et al. 2002). Informal surveys of several railroad corridors by the authors revealed large seed-bearing *Ailanthus* along railroad grades in Cambria, Dauphin, Lackawanna, Lycoming, and Philadelphia counties, among others, suggesting that railroad corridors continue to facilitate spread.

By 1925, the shift from railroads to highways as major means of transportation in the US made roadways important corridors for long-distance dispersal of seed. There was a noticeable increase in both incidence of large (>80 cm DBH) *Ailanthus* trees, as well as naturalized dense thickets of *Ailanthus* saplings, along PA highways at this time (Illick and Brouse 1926). Highways continue to play a profound role in spread and growth of invasive plant species, by providing a means of dissemination and an ideal disturbed habitat for seed germination and plant establishment (Mortensen et al. 2009).

Significant introduction of *Ailanthus* onto PA state forest lands did not occur until after 1950. It is likely that some lands purchased by the state during this time period already had established *Ailanthus* populations, and/or *Ailanthus* may have invaded state forest lands after purchase. *Ailanthus* may have existed on some of these lands prior to the 1950s either as single individuals, or as older cohorts with the oldest individuals representing the youngest surviving member of an otherwise extinct cohort. However, the majority of large *Ailanthus* trees cored during our study were >75 years of age, yet the presence of *Ailanthus* trees before 1950 were not detected within state forests, based on our increment core data. This finding suggests that the oldest sampled *Ailanthus* likely represent the first established specimens at each surveyed forest location, which is supported by personal observations of state foresters throughout PA (Table 3). The presence of *Ailanthus* trees >70 years in age in forests around Philadelphia (Table 1), as well as in Ohio's Tar Hollow State Forest (Joanne Rebbeck, USDA Forest Service, Delaware, OH, pers. comm.), clearly supports advanced age for *Ailanthus* within forest settings. Harvesting could explain attrition of older *Ailanthus* trees in our surveyed forest stands, but the prolific stump and root sprouting that occurs in *Ailanthus* following cutting would presumably have resulted in higher numbers of similar-aged individuals at the same locations, which was not the case. In addition, previous Verticillium wilt epidemics could have eliminated entire *Ailanthus* populations within PA state forests. Such wilt epidemics were reported in NYC and, to a lesser extent, Philadelphia in the late 1920s and early 1930s (Beach 1929, Gravatt and Clapper 1932). More recent Verticillium wilt epidemics have occurred in NY in the 1990s (Emmerich et al. 1998) and central PA in the early 2000s (Schall and Davis 2009a). Interestingly, none of the old Philadelphia trees contained false growth rings during the 1930s. False rings may be associated with *V. dahliae* rather than *V. nonalfalfae* infections, which suggests several likely possibilities: 1) infected trees ultimately died from the more virulent *V. nonalfalfae* and were not present in sampled populations; 2) *Verticillium* infection centers were geographically limited, and therefore not sampled in this study; or 3) false rings are only associated with light *Verticillium* infections during years when environmental conditions do not favor the pathogen, resulting in survival of infected *Ailanthus*. The presence of false rings in the oldest *Ailanthus* at one site in the Tuscarora State Forest offers some credibility to the third hypothesis (Appendix 4). Furthermore, our observations, as well as those of Schall and Davis (2009a, b) have revealed that *Ailanthus* is much more tolerant to *V. dahliae* than to *V. nonalfalfae*.

Widespread invasion of *Ailanthus* on PA state forest lands was generally not initiated until the late-1960s, with most establishment occurring after 1974 (Fig. 13b, Table 3). Although average stand age was not determined for all our sampled stands (Fig. 13), age estimations based on average diameters indicated that most dense *Ailanthus* thickets were fairly young (Table 3). Stand history records revealed that most (70%) forested stands with >1000 *Ailanthus* stems had been partially harvested or clearcut immediately prior to *Ailanthus* invasion. In addition, increment cores extracted from large *Ailanthus* trees within or immediately adjacent to harvested stands revealed year of establishment generally predated harvest (Table 3). Moreover, some pre-existing *Ailanthus* trees were bearing seed and were often growing up-wind of recently harvested stands, as with HSAa50 (Table 1, Table 3). Similarly, female *Ailanthus* trees at Bald Eagle State Forest, Tioga State Forest, and Tiadaghton State Forest produced seed responsible for invasion of nearby logging clear-cuts and abandoned railroad corridors (Table 3). The most significant *Ailanthus* invasions (including all locations with >5000 *Ailanthus* stems/location) closely followed large-scale clear-cuts in the aftermath of Oak Leaf Roller defoliation in the late 1960s and early 1970s, as well as subsequent salvage-logging following statewide Gypsy Moth defoliations in the 1980s. Logging operations in these defoliated stands were designed to salvage dead oaks, especially in oak-dominated stands that had suffered repeated defoliation and exhibited considerable oak mortality (Table 3; Herrick and Gansner 1988). Although *Ailanthus* was likely not present in all stands prior to harvest, the common size and type of harvest apparently led to widespread *Ailanthus* invasion. These findings suggest that clear-cutting and partial canopy removal associated with salvage-logging operations played an important role in fostering widespread invasion of *Ailanthus* into the cut-over sites (Table 3). Similarly, Carter and Fredericksen (2007) reported that *Ailanthus* seedlings tended to dominate recently logged, disturbed sites in southern VA, as compared to undisturbed mature forest stands. Similarly, Martin et al (2010) reported that *Ailanthus* grew 2.6 times faster than the fastest-growing native species in northwestern CT at 80% full sun but had some of the highest mortality rates in low-light conditions (1% full sun), which would likely limit this species to disturbed sites.

Although *Ailanthus* seedlings are only occasionally browsed by herbivores such as *Odocoileus virginianus* Zimmermann (White-tailed Deer), the level of browsing is significantly less in recently logged forests as compared to mature forests. This observation is likely related to the high number of *Ailanthus* stems in clear-cuts, which results in a significant number of non-browsed *Ailanthus* stems. In addition, heavy logging and clear-cutting result in numerous seedlings of more preferred plant species such as oaks and maples, which are browsed rather than *Ailanthus* seedlings (Carter and Fredericksen 2007, Williams et al. 2008). The lag between harvest and establishment of *Ailanthus* within the Bald Eagle State Forest and Michaux State Forest (Table 3) may suggest native regeneration failure followed by subsequent site colonization by *Ailanthus* seed. This scenario is likely influenced by heavy browsing of non-*Ailanthus* species in these areas by deer, reducing seedling density and delaying sapling growth of native species, leading to dominance of *Ailanthus* since this species is not preferred by deer (Augustine and McNaughton 1998, Carter and Fredericksen 2007, Gill and Beardall 2001).

Impacts of contemporary and future disturbances on expansion of *Ailanthus* in PA and beyond

The forests of PA are the result of long-term, dynamic stand-history patterns. However, their shared disturbance history has resulted in widespread invasion by *Ailanthus* and other invasive plant species. Large-scale natural disturbances such as insect defoliation and subsequent tree mortality, wildfire, and canopy gaps foster invasion by non-indigenous plants. In addition, anthropogenic disturbances such as logging, fires, surface mining, railroads and highway construction and corridors, etc. in proximity to established *Ailanthus* populations exacerbate the naturally occurring disturbances and may lead to widespread invasion across a number of forested sites. These interactions illustrate the importance of implementing preemptive stand-management strategies in our forests prior to overstory removal, as a means of limiting colonization by invasive plant species. Pennsylvania provides a strong case study for other states attempting to develop effective management strategies to limit colonization and range expansion by *Ailanthus* and other woody invasive species.

How Pennsylvania's forests and similar forests throughout the Northeast respond to contemporary and future disturbances, whether natural or anthropogenic, will depend on the severity and extent of those disturbances. However, the invasion of forests by exotic invasive plant species will not only continue, but will likely increase regardless of management strategy. There are numerous examples of shifts in forest tree species composition due to past insect infestations and disease epidemics. However, contemporary introductions of forest insects such as *Adelges tsugae* (Annand) (Hemlock Woolly Adelgid [HWA]), *Anoplophora glabripennis* (Motschulsky) (Asian Long-horned Beetle), and *Agrilus planipennis* Fairmaire (Emerald Ash Borer), as well as fungal pathogens such as *Geosmithia morbida* (M. Kolarík, E. Freeland, C. Utley, and Tisserat) and *Raffaelea lauricola* T.C. Harr., Fraedrich, and Aghayeva, causal agents of Thousand Cankers Disease and Laurel Wilt, respectively, may cause additional widespread changes in the structure and composition of our forests, ultimately opening these stands and favoring invasion by exotic plant species. Orwig and Foster (1998) observed that *Ailanthus* rapidly invaded *Tsuga canadensis* (L.) Carr. (Eastern Hemlock) stands exhibiting moderate to severe mortality following HWA infestations in CT. Similarly, hemlock stands killed by HWA in PA, the Mid-Atlantic region, and areas further south will likely experience significant invasions by *Ailanthus* and other non-indigenous plants. Widespread invasions are likely to occur in areas where large populations of *Ailanthus* are currently growing in close proximity to devastated hemlock stands such as in the Delaware Water Gap National Recreation Area (DEWA). Indeed, Eichelberger and Perles (2009) reported that numerous hemlock stands at DEWA killed by HWA infestations were susceptible to invasion by exotic plant species such as *Ailanthus*. These authors also reported that *Ailanthus* was already present in 20% of DEWA, including areas that contained hemlock communities. Fortunately, many of the intact DEWA hemlock stands are not suitable habitats for *Ailanthus*, due to limited edge openings, low soil pH, and dense canopies from remaining hardwood associates (Eichelberger and Perles 2009). Yet, declining hemlock stands outside the intact hemlock forests were considered vulnerable to invasion by *Ailanthus*, especially near roadways and disturbed areas. Furthermore, as hemlock mortality continues, soil pH may gradually increase, favoring future *Ailanthus* invasions. In support of this contention, we recently observed *Ailanthus* invading HWA-killed hemlock stands near the Rothrock State Forest adjacent to a major roadway.

Zomlefer et al. (2008) observed significant mortality of *Persea borbonia* (L.) Spreng. (Redbay) and *Sassafras albidum* (Nutt.) Nees (Sassafras) on Cumberland Island, GA, caused by the laurel wilt fungal pathogen, *Raffaelea lauricola.* Laurel wilt has resulted in significant losses of Redbay and Sassafras, as well as other species, along roadways and within various coastal forest communities. Concurrently, Zomlefer and colleagues (2008) documented *Ailanthus* invading disturbed areas on Cumberland Island. Although the *Ailanthus* abundance in the area was relatively low, widespread site disturbance following Redbay mortality will likely provide new opportunities for *Ailanthus* invasion, especially along roadways where Redbay was a co-dominant tree in the canopy. Although Redbay is not native to the northeastern US, Sassafras is abundant throughout the Mid-Atlantic, where it prefers disturbed sites, abandoned fields, fence rows, and dry ridges and upper slopes (Griggs 1990). Widespread mortality of Sassafras by *R. lauricola* could favor supplantation by *Ailanthus* in areas where the two species' ranges overlap.

Exceptional disturbances, such as the catastrophic flooding in PA during 2011 following Tropical Storm Lee*,* increase the likelihood of riverbanks and flood plains being invaded by *Ailanthus*. For example, seed-bearing *Ailanthus* trees identified in our floristic survey were growing in a large cluster along a feeder creek of the Susquehanna River in Bradford County. In September 2011, flood waters downed hundreds of trees including seed-bearing *Ailanthus*, which were subsequently washed into the Susquehanna River. Large numbers of *Ailanthus* seeds were transported along the downstream river corridor, which will likely result in establishment of new *Ailanthus* seedlings along the riverbanks and at other areas within the floodplain. In a related study, Kaproth and McGraw (2008) reported that *Ailanthus* seeds dispersed directly into water can travel long distances and readily germinate, even after prolonged inundation up to 5 months. This study suggests that those seeds swept by the floods will likely survive a prolonged period in floodwaters, allowing *Ailanthus* seedlings to readily establish on stream banks or in flood plains once waters have rescinded.

Some of the most serious impacts currently facing PA forests are from drilling activities to extract and transport natural gas from the Marcellus Shale Formation. Widespread land-clearing, road building, and pipeline establishment related to natural-gas drilling activities have resulted in an unprecedented increase in incidence of disturbed areas ideal for invasion by exotic plants. Considerable Marcellus Shale drilling activities are currently taking place in the northern tier counties of PA, where *Ailanthus* is currently absent or occurs at low levels. Northern tier counties that contain few if any *Ailanthus* include McKean, Potter, Susquehanna, and, except for Blackwell, most of Tioga (Fig. 14). Some localized *Ailanthus* populations have been identified in Bradford and Warren counties, but lack suitable disturbed sites for widespread invasion aside from flood plains and riverbanks. However, natural-gas drilling activities will likely furnish a plethora of disturbed sites ideal for *Ailanthus* invasion from the few natural seed sources in the area. In addition, some activities associated with the drilling, extraction, and transportation of natural gas require crushed stone or gravel (NYDEC 2009). If gravel is brought in from south of the northern tier counties, there is the added risk that these materials, or the vehicles used to transport them, may harbor seeds from *Ailanthus* as well as other invasive species, which could become established within the disturbed sites. Movement of new *Ailanthus* populations into the PA northern tier counties is likely as the connectivity of viable habitat patches increases (Hellmann et al. 2008). This expansion, in addition to the northward migration of tree species such as *Ailanthus* due to global climate change, may drastically alter the future geographic range of *Ailanthus*.

With regard to climate change, the distribution of *Ailanthus* in PA clearly shows that few *Ailanthus* populations have been documented in USDA Plant Hardiness Zone 5a and 5b, a zone comprising the northern tier of PA with average annual minimum temperatures of below -23°C (Fig. 15). The scarcity of *Ailanthus* in this geographic region of PA, including complete absence of *Ailanthus* from Elk, Forest, McKean, and Susquehanna counties, which are mainly within Hardiness Zone 5, suggests that the low temperatures, perhaps coupled with minimal forest fragmentation and development are likely limiting *Ailanthus* establishment and spread in this area (Fig. 15). However, our recent discovery of a 50-year old *Ailanthus* in Tioga County, as well as the persistence of *Ailanthus* in Bradford, Crawford, and Warren counties suggests that Hardiness Zone 5b has sustained *Ailanthus* populations during the past several decades. In contrast, evidence of early 20th-century plantings of *Ailanthus* in Potter County could not be found, suggesting that conditions unfavorable to *Ailanthus* (e.g., exceptionally cold winters) probably eliminated this species from these areas sometime after 1925. Our observations of patterns of *Ailanthus*' spread further south in PA suggest that incidence of *Ailanthus* in northern PA will likely increase in close proximity to already established *Ailanthus* populations at a faster rate compared to establishment of novel outlier populations.

Conclusions

Ailanthus has a long history in PA, yet widespread invasion by this species was not apparent until the last decades of the 20th century. These observations reflect salvage logging practices following unprecedented mortality of canopy oaks in the aftermath of state-wide Gypsy Moth outbreaks in the early 1980s. Tree-ring studies revealed *Ailanthus* can exceed 100 years of age, yet many *Ailanthus* stands, particularly in PA forests, are very young, and maximum age limits are unknown for this species in a natural forest environment. Although no early plantings were found in our recent surveys due to age limitation, extant

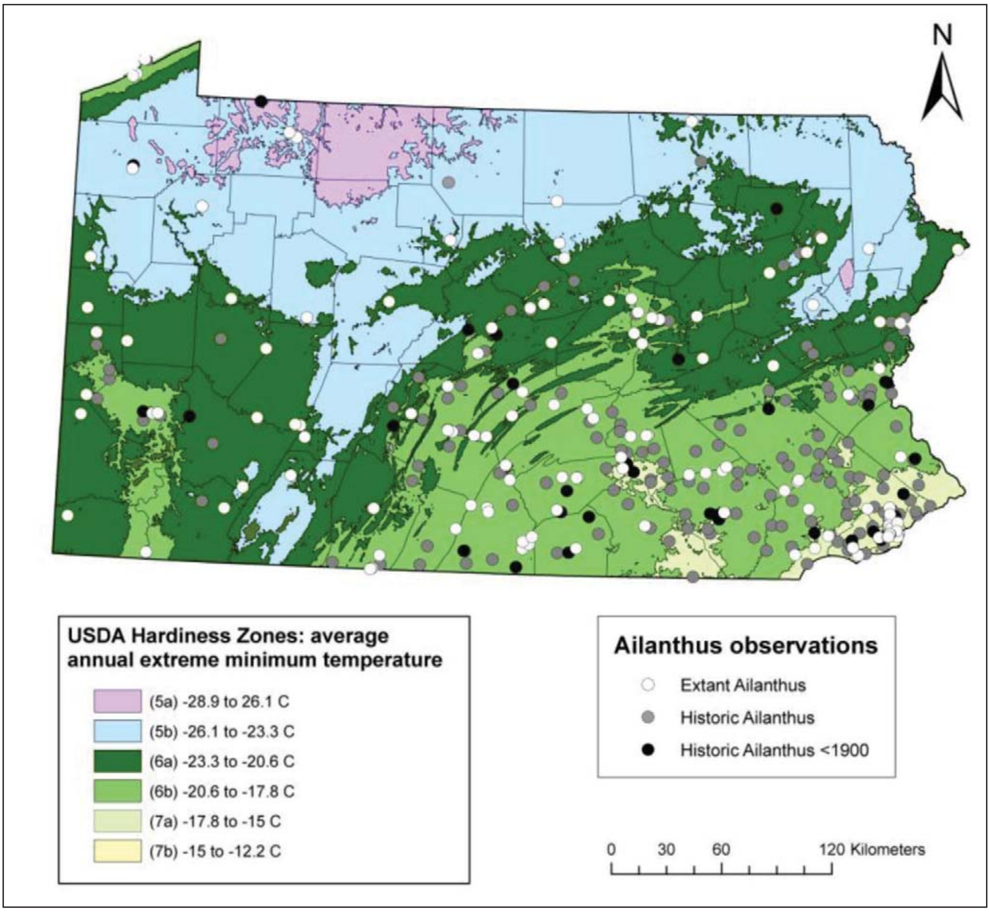

Figure 15. Historic and contemporary *Ailanthus* distribution in PA overlaid onto the 2012 USDA hardiness zone map. *Ailanthus* points include historic observations (gray circles) such as previous flora surveys, herbarium specimens, and from reputable historic publications, as well as our most recent survey (white circles) conducted between 2010–2011. See Appendix 5 for locations of extant *Ailanthus*. Historic points (gray circles) provided by paflora.org.

individuals were found in a number of historic locations, where tree-rings and associated age-prediction models were able to help resolve spatial and temporal migration patterns and establish areas of continuous colonization within PA including Bartram's Garden in Philadelphia. Furthermore, these studies support establishment of *Ailanthus* in several PA counties 70–118 years earlier than previously reported. Although *Ailanthus* is generally widespread throughout PA, there are still many areas vulnerable to invasion, where cold temperatures and minimally disturbed areas have limited *Ailanthus* invasion. Although *Ailanthus* has been eradicated in a few sites, most land managers and private landowners in PA are losing the battle to control the spread of this highly invasive tree species. In the future, land and forest managers should consider various facets of *Ailanthus* biology and invasion history, as revealed in this monograph, to better formulate management decisions.

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Appendix 1. Year of first report of *Ailanthus altissima* by county and associated references.

County	Year^{A}	Reference^{B}
Adams	1925	Illick and Brouse 1926
Allegheny	1842	Wardrop 1842
Armstrong	1970	Wherry et al. 1979
Beaver	1915	Archives of the Plant Disease Clinic, The Pennsylvania State University
Bedford	1970	Wherry et al. 1979
Berks	1892	The Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia, PA (uncharacterized, no accession #)
Blair	1852	Smithsonian Institute 1861
Bradford	2004	McWilliams et al. 2007
Bucks	1905	Moyer 1905
Cambria	1925	Illick and Brouse 1926
Carbon	1970	Wherry et al. 1979
Centre	1851	Smithsonian Institute 1861
Chester	1820	Darlington, 1853
Clinton	1993	Rhoads and Klein 1993
Crawford	1852	Smithsonian Institute 1861
Cumberland	1925	Illick and Brouse 1926
Dauphin	1924	Philips 1924
Delaware	1852	Smithsonian Institute 1861
Erie	1923	Miller 1923
Franklin	1914	Illick 1914 (Pennsylvania Trees, Bulletin 11)
Fulton	1970	Wherry et al. 1979
Greene	2004	McWilliams et al. 2007
Huntingdon	1960	The Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia, PA
Jefferson	2004	McWilliams et al. 2007
Juniata	1970	Wherry et al. 1979
Lackawanna	1887	Dudley 1887
Lancaster	1837	Sargent 1878
Lebanon	1970	Wherry et al. 1979
Lehigh	1938	The Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia, PA (Accession No. 16659)
Luzerne	1905	The Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia, PA (Accession No. 689227)
Lycoming	1905	Gearhart 1907
Mifflin	1889	New York Botanical Garden Steere Herbarium, Bronx, NY
Mercer	2004	McWilliams et al. 2007
Montgomery	1893	Harvey 1895
Montour	1970	Wherry et al. 1979

County	Year[A]	Reference[B]
Northampton	1852	US Senate 1864 (Report of the Commissioner of Patents on meteorological observations, 1854–1859)
Northumberland	1849	The Philadelphia Herbarium at the Academy of Natural Sciences, Philadelphia, PA
Perry	1907	De la Hunt 1916
Philadelphia	1784	Browne 1846
Potter	1925	Illick and Brouse 1926
Schuylkill	2004	McWilliams et al. 2007
Snyder	1905	Gearhart 1907
Tioga	2004	McWilliams et al. 2007
Union	1905	Gearhart 1907
Warren	1891	Illick and Brouse 1926
Westmoreland	1857	Smithsonian Institute 1861
Wyoming	1988	Clark 1991
York	1874	Riley 1874

[A] Year refers to the the earliest published report for a specific county. Many counties have multiple published reports and herbarium specimens supporting these early dates but were excluded from this table.

[B] Reference material includes historic reports and publications, collections from herbaria, recent collections of plant material by corresponding author, and estimates derived using linear regression.

Appendix 2. Location, county, year, and diameter for historic observations on *Ailanthus* in Pennsylvania. Year = year of observation.

Location	County	Year[A]	DBH (cm)[B]	Reference
Aldie Mansion	Bucks	1993	144.0	Hobaugh 1993
Awbury Arboreteum	Philadelphia	1988	136.7	Clark 1988
Bartram's Garden	Philadelphia	1809	0.0*	Browne 1846
	Philadelphia	1834	40.4**	Breck 1837
	Philadelphia	1846	53.3**	Browne 1846
	Philadelphia	1853	67.8**	Meehan 1853
	Philadelphia	1855	67.8	Barry and Smith 1855
	Philadelphia	1877	90.7**	Sargent 1878
	Philadelphia	1897	0.0	Wilson 1897
	Philadelphia	1907	0.0	JBA 1907
	Philadelphia	1919	71.1	Anonymous 1919
	Philadelphia	1937	106.7	Anonymous 1937
	Philadelphia	1970	0.0	Swartley 1970
	Philadelphia	1983	0.0	Palmer 1983
	Philadelphia	2010	38.9	M. Kasson, pers. observ.
Grumblethorpe	Philadelphia	1830	0.0*	Jellett 1904
	Philadelphia	1904	118.1**	Jellett 1904
	Philadelphia	1909	0.0	Eastwick 1963
Independence Square	Philadelphia	2009	0.0	Smith 2009
Lemon Hill Mansion	Philadelphia	1845	0.0	Dwight 1845
Longwood Gardens	Chester	2010	88.1	Wade 2011
Marshall's Garden	Chester	1820	0.0*	Darlington 1853
	Chester	1893	0.0	Sargent 1893
	Chester	1899	0.0	Harshberger 1899
	Chester	1920	0.0	Harshberger 1921
	Chester	1893	0.0	Sargent 1893
	Chester	1899	0.0	Harshberger 1899
	Chester	1920	0.0	Harshberger 1921
	Chester	1925	61.0	Illick and Brouse 1926
	Chester	1925	76.2	Illick and Brouse 1926
	Chester	1958	87.4	Belden 1958
Woodlands	Philadelphia	1785	0.0	Browne 1846
	Philadelphia	1790	0.0*	Smith 1905
	Philadelphia	1921	0.0	Harshberger 1921
Other	Philadelphia	1827	0.0*	Jones 1835
	Philadelphia	1827	0.0*	Jones 1835
	Philadelphia	1827	0.0*	Jones 1835
	Philadelphia	1827	0.0*	Jones 1835
	Adams	1833	0.0	Wentz 1950
	Philadelphia	1835	25.7	Jones 1835
	Philadelphia	1835	27.4**	Jones 1835
	Philadelphia	1835	23.9**	Jones 1835
	Philadelphia	1835	23.4**	Jones 1835
	Lancaster	1837	0.0*	Sargent 1878
	Lancaster	1837	0.0*	Sargent 1878
	Lancaster	1868	45.7**	Sargent 1878
	Lancaster	1868	45.7**	Sargent 1878
	Lancaster	1877	51.8**	Sargent 1878

Location	County	Year[A]	DBH (cm)[B]	Reference
	Lancaster	1877	54.9**	Sargent 1878
	Philadelphia	1904	76.2	Jellett 1904
	Philadelphia	1904	0.0	Jellett 1904
	Dauphin	1924	83.8	Phillips 1924
	Cumberland	1925	76.2	Illick and Brouse 1926
	Franklin	1925	103.6	Illick and Brouse 1926
	Cumberland	1925	106.7	Illick and Brouse 1926
	Cumberland	1925	97.5	Illick and Brouse 1926
	Cumberland	1925	97.5	Illick and Brouse 1926
	Cumberland	1925	85.3	Illick and Brouse 1926
	Cumberland	1925	82.3	Illick and Brouse 1926
	Cumberland	1925	91.4	Illick and Brouse 1926
	Franklin	1925	97.5	Illick and Brouse 1926
	Adams	1925	91.4	Illick and Brouse 1926
	Chester	1925	61.0	Illick and Brouse 1926
	Chester	1925	61.0	Illick and Brouse 1926
	Adams	1925	81.3	Photo Archives of the Lutheran Theological Seminary, Gettysburg, PA
	Adams	1925	63.5	Photo Archives of the Lutheran Theological Seminary, Gettysburg, PA
Other	Adams	1925	63.5	Photo Archives of the Lutheran Theological Seminary, Gettysburg, PA
	Adams	1950	0.0	Wentz 1950
	Dauphin	1968	122.2	Mickalitis 1969
	Dauphin	1978	127.0	Hill 1986
	Lebanon	1988*	126.2	Clark 1988
	Philadelphia	1988	136.6	Clark 1988
	Wyoming	1990	137.4	Clark 1991
	Delaware	2008	71.1	Wade 2011

[A] Date of observation: the 126.2-cm-diameter *Ailanthus* reported in Lebanon County had a year of most recent measurement in 1900. This appears to be a gross error given this observation was published in 1988.

[B] All measurements reported were converted to diameter in centimeters. If measurements were excluded from a specific reference, a value of 0.0 was given. Those 0.0 values followed by * denote a reported planting date at a specific location. **denotes historic measurements used in developing linear regression to predict age based on DBH (Fig. 12).

Appendix 3. Age prediction validation using two approaches on intact large *Ailanthus*. Age predictions are by average ring width at several decay intervals (%)[A]

			Age by linear	Age predictions					
Tree ID	DBH	Age	regression	85	75	65	50	25	5
HSAa42	59.4	34	48	20	20	29	36	35	32
HSAa36	43.2	41	33	47	52	51	48	43	41
HSAa19	80.0	42	67	40	48	51	50	47	43
HSAa20	39.9	48	29	47	52	49	52	49	51
HSAa32	50.0	59	39	107	96	100	90	71	59
HSAa28	74.4	61	62	47	52	57	58	64	61
HSAa46	126.5	64	110	40	44	51	66	69	64
HSAa27	62.0	77	50	60	84	86	90	81	79
HSAa08	85.9	79	72	60	60	69	88	93	82
HSAa38	98.3	79	84	127	124	117	100	84	76
HSAa13	100.6	80	86	153	140	117	110	100	86
HSAa04	72.1	83	59	87	140	143	128	107	89
HSAa15	87.9	84	74	93	84	83	78	80	84
HSAa44	85.6	96	72	180	172	151	132	113	95
HSAa29	108.5	107	93	80	84	89	108	111	104
HSAa11	132.6	117	116	127	112	117	138	133	119

[A] Mean ring width predictions were determined by counting total rings for each decay class and then taking the average ring width (core width/total rings) to project the number of rings over the length of the missing section.

Appendix 4. Incidence and distribution of false rings (FR) in *Ailanthus* in PA and OH[A].

Increment core ID[B]	First ring[C]	No. FR	Year and incidence of false-ring formation in *Ailanthus* annual growth increment cores[D]
HSAa02A1	1979	2	1991, 1982
HSAa03A1	1923	15	2008 (2)*, 2007, 2006*, 2004, 2002 (2), 1997, 1996, 1995*, 1993 (2), 1987, 1980
HSAa03B1	1930	7	2006*, 1997*, 1996, 1995 (2), 1994, 1989
HSAa03C1	1973	15	2010, 2008*, 2007, 2005, 2004, 2001, 1998 (2), 1997 (2), 1996, 1993 (2), 1988, 1987
HSAa08A1	1932	1	1974
HSAa09D1	1994	5	2010 (3), 2009 (2)
HSAa11A1	1899	8	2009 (2), 1989*, 1988, 1986 (2), 1984, 1980
HSAa11B1	1895	2	2003, 1903
HSAa12B1	1992	2	1995 (2)
HSAa18A1	1952	1	1988
HSAa23A1	1923	3	1998, 1997, 1933
HSAa25A1	1954	2	2003*, 1999*, 1998
HSAa27A1	1931	5	1996 (3), 1957 (2)
HSAa29A1	1904	2	2010, 2009
HSAa29B1	1910	1	2010
HSAa32A1	1953	1	2004
HSAa35A1	1960	1	1985
HSAa40B1	1939	1	1980
HSAa42A1	1979	1	2008
HSAa43B1	1929	2	1999, 1996
HSAa45D1	1966	3	2009, 2006 (2)
HSAa47A1	1907	1	1999
Vd-1-06-232*	1984	2	2009*, 2006*
Vd-1-06-242*	1990	2	2006*
RLK-443	1966	13	2004, 2002, 2001, 1999, 1997 (2), 1996, 1995 (3), 1987, 1978 (2)
RLKb-443**	1976	1	1995
F88-2A4	1960	5	2004, 1995 (3), 1981
F81-1C4	1979	1	2008
GP201-2AB4	1989	1	2008
F-86-1AB4	1973	1	1983

[A] General location includes *Ailanthus* trees primarily from large-tree study and three other forested locations where peripheral studies are being conducted.

[B] Trees include individuals from (1) Table 1, (2) Tuscarora SF, Perry County, PA, (3) ACOE Raystown Lake, Huntingdon Co., PA, or (4) Tar Hollow SF, Jefferson Co., OH. Trees were either inoculated (*) with *Verticillium dahliae* in 2006 or confirmed as having natural infections (**) of *Verticillium dahliae* in 2009.

[C] First ring refers to the year of the first measurable annual growth ring for that particular core.

[D] A * following individual ring numbers indicates vascular discoloration preceded false-ring formation.

Appendix 5. Pennsylvania *Ailanthus* trees included in 2010–2011 floristic survey.

Tree ID	Tissue[A]	Environment	County	City/Location	Collected	Collector
P001	Leaf	Urban	Erie	Erie	06/19/10	M.T. Kasson
P002	Leaf	Wooded Urban	Erie	Erie	06/19/10	M.T. Kasson
P003	Leaf	State Park	Erie	Erie	06/19/10	M.T. Kasson
P004	Leaf	Urban	Venango	Oil City	06/19/10	M.T. Kasson
P005	Leaf	Park	Allegheny	Pittsburgh	06/20/10	M.T. Kasson
P006	Leaf	SGL #117	Washington	Burgettstown	06/20/10	M.T. Kasson
P007	Leaf	Forest	Huntingdon	Raystown Lake	06/21/10	M.T. Kasson
P008	Leaf	Roadside	Bedford	Bedford	06/21/10	M.T. Kasson
P009	Leaf	State Park Forest	Blair	Canoe Creek SP	06/21/10	M.T. Kasson
P010	Leaf	Roadside	Huntington	Mt. Union	06/22/10	M.T. Kasson
P011	Leaf	Roadside	Perry	East Salem area	06/22/10	M.T. Kasson
P012	Leaf	Forest	Dauphin	SGL #211	06/22/10	M.T. Kasson
P013	Leaf	Roadside	Franklin	Mont Alto	06/23/10	M.T. Kasson
P014	Leaf	Forest	Franklin	Buchanan SF	06/23/10	M.T. Kasson
P015	Leaf	Forest	Somerset	Boswell	06/23/10	D.D. Davis
P016	Leaf	Roadside	Pike	Matamoris	06/26/10	M.T. Kasson
P017	Leaf	Urban	Lackawanna	Scranton	06/26/10	M.T. Kasson
P018	Leaf	Urban	Cambria	Johnstown	06/26/10	D.D. Davis
P019	Leaf	Roadside	Indiana	Blairsville	06/26/10	D.D. Davis
P020	Leaf	RR tracks	Westmoreland	Seward	06/26/10	D.D. Davis
P021	Leaf	Urban	Mifflin	Lewistown	06/28/10	M.T. Kasson
P022	Leaf	Roadside	Juniata	Port Royal	06/29/10	M.T. Kasson
P023	Leaf	Roadside	Clearfield	Clearfield	07/01/10	D.D. Davis
P024	Leaf	Roadside	Jefferson	Punxsutawney	07/03/10	D.D. Davis
P025	Leaf	Roadside	Armstrong	Sagamore	07/14/10	D.D. Davis
P026	Leaf	Forest	Lycoming		07/21/10	E.S. O'Neal
P027	Leaf	Roadside	Luzerne	Dupont	07/24/10	M.T. Kasson
P028	Leaf	River bank	Warren	Warren	07/21/10	R.P. Long
P029	Both	PA turnpike	Lebanon		07/30/10	M.T. Kasson
P030	Both	Roadside	Adams	Gettysburg	07/30/10	M.T. Kasson
P031	Both	Urban	York	York	07/30/10	M.T. Kasson
P032	Leaf	PA turnpike	Berks		07/30/10	M.T. Kasson
P033	Both	Roadside	Delaware	Chester	07/30/10	M.T. Kasson
P034	Both	PA turnpike	Montgomery		07/30/10	M.T. Kasson
P037	Seed	Roadside	Chester		07/30/10	M.T. Kasson
P038	Leaf	Roadside	Cumberland		07/30/10	M.T. Kasson
P039	Both	Roadside	Cumberland	Camp Hill	07/30/10	M.T. Kasson
P040	Leaf	RR tracks	Lancaster	Downingtown	07/30/10	M.T. Kasson
P041	Seed	Industrial	Lancaster	Downingtown	07/30/10	M.T. Kasson
P042	Leaf	Forest	Chester	West Chester	07/30/10	G. Hertel
P043	Leaf	I-80 E	Clinton		08/12/10	M.T. Kasson
P044	Both	I-80 E	Snyder		08/12/10	M.T. Kasson
P045	Both	I-80 E	Clinton		08/11/10	Tim Frontz
P047	Both	Urban	Northumberland	Mt. Carmel	08/12/10	M.T. Kasson
P048	Leaf	Roadside	Lehigh	Allentown area	08/12/10	M.T. Kasson
P049	Leaf	Roadside	Schuylkill		08/12/10	M.T. Kasson
P050	Leaf	Roadside	Monroe	Snyderville	08/12/10	M.T. Kasson
P051	Leaf	Roadside	Northampton	Nazareth	08/12/10	M.T. Kasson
P052	Leaf	I-80 E	Montour		08/12/10	M.T. Kasson
P053	Both	Roadside	Union	Lewisburg	08/12/10	M.T. Kasson

Tree ID	Tissue[A]	Environment	County	City/Location	Collected	Collector
P054	Leaf	Urban	Carbon		08/12/10	M.T. Kasson
P055	Leaf	Roadside	Cameron		08/06/10	T. Frontz
P056	Leaf	Roadside	Butler		08/09/10	T. Frontz
P057	Leaf	Forest	Beaver		08/20/10	E. Rosko
P058	Leaf	I-80 E	Montour		08/31/10	T. Frontz
P059	Leaf	Substation	Crawford	Meadville	09/02/10	T. Frontz
P060	Both	Roadside	Lawrence		08/30/10	T. Frontz
P061	Leaf	Roadside	Union		08/31/10	T. Frontz
P062	Leaf	Roadside	Clarion		09/01/10	T. Frontz
P063	Leaf	I-80 E	Mercer		09/02/10	T. Frontz
P064	Both	Roadside	Northumberland	Milton area	08/31/10	T. Frontz
P065	Seed	Roadside	Centre	Bellefonte	09/20/10	M.T. Kasson
P066	Both	PA turnpike	Beaver		09/23/10	T. Frontz
P067	Leaf	Roadside	Fayette	Normalville	10/06/10	D.D. Davis
P068	Leaf	Forest	Delaware	Aston	10/12/10	M.T. Kasson
P071	Leaf	Roadside	Perry	Millerstown	10/15/10	M.T. Kasson
P072	Leaf	Roadside	Perry	Newport	10/15/10	M.T. Kasson
P073	Leaf	Roadside	Fulton	McConnellsburg	10/15/10	M.T. Kasson
P074	Leaf	Forest	Franklin	Buchanan SF	10/30/10	M.T. Kasson
P076	Leaf	Frick Park, Forest	Allegheny	Pittsburgh	11/07/10	M.T. Kasson
P077	Leaf	Forest	Huntington	ACOE forest	11/03/10	M.T. Kasson
P078	Leaf	Forest	Huntington	ACOE forest	11/03/10	M.T. Kasson
P082	Leaf	Rail trail	Lycoming	Waterville	11/15/11	M.T. Kasson
P083	Leaf	Rail trail	Tioga	Blackwell	11/15/11	M.T. Kasson
P084	Seed	Riverbank	Bradford	Athens	11/17/11	M.T. Kasson
P085	Leaf	Roadside	Wayne		06/26/10	M.T. Kasson
P086	Seed	Roadside	Greene		08/08/11	S. Coons
P087	Seed	Roadside	Greene		08/08/11	S. Coons
S020	Seed	Forest	Franklin	Tuscarora SF	09/04/07	M.J. Schall
S038	Seed	Forest	Franklin	Buchanan SF	10/09/09	M.T. Kasson
W01	Wood	Roadside	Indiana	Cramer	10/9/11	M.T. Kasson
W02	Wood	forest	Centre	Bald Eagle SF	11/10/11	M.T. Kasson
W03	Wood	forest	Berks	French Creek SP	11/17/11	M.T. Kasson
W04	Wood	Forest	Huntingdon	Rothrock SF	11/10/11	M.T. Kasson
W05	Wood	Forest	Cumberland	Michaux SF	11/10/11	M.T. Kasson
W06	Wood	Forest	Mifflin	Tuscarora SF	11/10/11	M.T. Kasson
W07	Wood	Forest	Perry	Tuscarora SF	12/2/11	M.T. Kasson
W08	Wood	Forest	Mifflin	Tuscarora SF	12/2/11	M.T. Kasson
W09	Wood	Forest	Franklin	Tuscarora SF	11/10/11	M.T. Kasson

[A] Tissue refers to specific tissues collected at each location. Both refers to leaf plus seed. DNA was extracted from both leaf and seed tissue for a related study. Cross-sections and cores were sampled for tree-ring analysis (see Fig. 14).