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Distribution and demographics of *Ailanthus altissima* in an oak forest landscape managed with timber harvesting and prescribed fire

Joanne Rebbeck *, Todd Hutchinson, Louis Iverson, Daniel Yaussy, Timothy Fox

USDA Forest Service, Northern Research Station, 359 Main Road, Delaware, OH 43015, United States

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ABSTRACT

Ailanthus altissima ((Mill.) Swingle, tree-of-heaven), an exotic invasive tree that is common throughout much of the eastern United States, can invade and expand dramatically when forests are disturbed. Anecdotal evidence suggests that fire facilitates its spread, but the relationship between fire and this prolific invasive tree is poorly understood. To better understand the impacts of fire on *Ailanthus*, we conducted studies at Tar Hollow State Forest in southeastern Ohio, where *Ailanthus* is widely distributed and where, since 2001, prescribed fire has been applied to 25% of the 3885-ha study area. Our objective was to gain a better understanding of how the distribution and abundance of *Ailanthus* is related to recent fires, harvesting activity, and site characteristics. We quantified the abundance and demography of *Ailanthus*, as well as prescribed fire, harvesting, aspect, slope, and available light, using a systematic grid (400 m) of sample plots (N = 267). From these data, we identified time since last timber harvest, not prescribed fire history, as the major driver of both *Ailanthus* seedling and tree presence and density. Two site factors, aspect index (a transformation of aspect) and photosynthetically active radiation, were also significant predictors of seedling presence or density. These findings to demonstrate that dormant-season prescribed fire has a limited impact on the distribution of *Ailanthus* within forested landscapes and that recent timber harvesting (within 20 years) is the primary predictor. Thus, care in harvesting to prevent soil disturbance and spread of *Ailanthus* seed is paramount when managing for this aggressive species.

1. Introduction

Throughout much of the Central Hardwoods region of the eastern United States, the sustainability of oak forests is threatened by poor regeneration and ever-increasing abundances of shade-tolerant and fire-sensitive tree species. Given that fire was an important process historically (Guyette et al., 2002), the use of prescribed fire to sustain oak ecosystems has been widely promoted and is now being used more frequently as a management tool (Dickinson, 2006). Many national forests in the eastern United States have determined that sustaining oak forests as an important objective in their revised Forest Management Plans (Yaussy et al., 2008). Many state agencies are also embracing the use of prescribed fire to sustain mixed oak forests, enhance wildlife habitat, and reduce fuel buildup. While a long-term regime of prescribed fire combined with forest thinning can favor oak regeneration, this practice may also increase the risk for the invasion and expansion of non-native plant species such as the highly invasive, *Ailanthus* that is widely distributed in the eastern United States and elsewhere in the world (Sladonja et al., 2015).

Fire has often been shown to favor non-native invasive species in the western United States (Zouher et al., 2008). In the eastern United States, nonnative invasive species are becoming increasingly abundant (Dibble et al., 2008) and are a major management concern, especially under a changing climate (Dukes et al., 2009). However, because large and high severity wildfires are infrequent and the widespread use of prescribed burning has begun only recently, much less is known about the effects of fire on invasives in this region (Gucker et al., 2012). Results from limited studies and anecdotal information suggest that wildfire may increase *Ailanthus* density in North America (Pomp, 2008; Guthrie et al., 2016). In the Insubric region of the southern Swiss Alps, Maringer et al. (2012) documented that *Ailanthus* and black locust (*Robinia pseudoacacia*) invaded and grew in high abundance within areas of high-light and bare soil created following a high intensity wildfire. Understanding how nonnative tree species respond to fire, timber harvesting and site characteristics across large forested landscapes is crucial to improve practices to limit dispersal and invasion.

Ailanthus is a deciduous tree native to northeastern China that has developed into an invasive species expanding on all continents

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* Corresponding author.
E-mail address: jrebbeck@fs.fed.us (J. Rebbeck).

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except Antarctica (Kowarik and Säumel, 2007). It was introduced as an ornamental tree in France during the 1740s, with rapid distribution to other parts of Europe (Kowarik and Säumel, 2007). *Ailanthus* was brought to North America via Philadelphia in 1784 and its expansion to other areas quickly followed (Kasson et al., 2013). It is a dioecious tree which can invade disturbed habitats via establishment from abundant wind-dispersed seed and clonal ramets. *Ailanthus* is capable of aggressive clonal spread, which can result in dense thickets. It is fast growing, reaching heights of 18–21 m in 10 years (Knapp and Canham, 2000; Kowarik and Säumel, 2007). While typically classified as an early-successional, gap-obligate and shade-intolerant species, Knüsel et al., 2017 found that relatively low light conditions were sufficient for growth and survival of regenerating Ailanthus. Martin et al. (2010) demonstrated that despite high growth rates, *Ailanthus* had poor survivorship in low light environments. Clonal sprouts attached to a parent tree can persist in a shaded forest understory for up to 20 years (Kowarik, 1995; Knapp and Canham, 2000). Annual seed production rates exceeding 300,000 seeds per female tree are not unusual (Bory and Clair-Maczulajtys, 1980). However, published data documenting how far *Ailanthus* seeds can travel is limited (Kowarik and Säumel, 2007; Landenberger et al., 2007). Kota (2005) reported that wind dispersed seeds traveled at least 200 m.

Currently, *Ailanthus* is present in many eastern U.S. forested landscapes (Ellenwood et al., 2015) where the use of prescribed fire to favor oak regeneration is increasing. *Ailanthus* is most often abundant in open sites such as roadsides (McAvoy et al., 2012) but it frequently invades and establishes within disturbed forest sites. Little is known about the demographics of *Ailanthus* within actively managed forests where prescribed fires are applied. Given that *Ailanthus* is widely distributed throughout eastern US and many European forests, and is difficult and costly to control chemically, it is crucial to have a better understanding of how *Ailanthus* responds to timber management practices, including fire and harvesting regimes.

We witnessed the abundant establishment of *Ailanthus* seedlings following a shelterwood thinning and prescribed fire treatment on 26-ha unit at Tar Hollow State Forest (THSF; 39 °21′N; 82 °46′W) located in southeastern Ohio. THSF was one of the three Ohio Hill network sites of the national Joint Fire Science Program (JFSP) Fire and Fire Surrogate Study (Rebbeck et al., 2005; McIver et al., 2012). Within the 26-ha prescribed burn + thinning treatment unit, it appears that the combination of an ample seed source (via a few fecund adult females) along with soil and canopy disturbances (including dispersal via large machinery) during installation of the shelterwood harvest caused the observed increase in *Ailanthus* seedlings. This was further supported by a post-treatment inventory that found few if any adult female *Ailanthus* present in the two adjacent 20-ha treatment units (shelterwood-only and burn-only) and no observed large post-treatment increases in *Ailanthus* (Hutchinson et al., 2004).

Our goal was to gain a better understanding of how the distribution and abundance of *Ailanthus* is related to recent prescribed fires, harvesting activity, and landscape features. Our primary objective was to determine if recent prescribed fires would increase the occurrence of *Ailanthus* across a managed forest landscape with dissected topography. Secondly, to determine the effects of timber harvesting on *Ailanthus* abundance. To accomplish this, we used historic timber management records and *Ailanthus* demographic data collected in a systematic grid across the 3885-ha study area of which 25% had been treated with prescribed fire within the previous seven years. Ultimately, we sought to increase our understanding of the ecology of this aggressive invasive so that management practices directed at minimizing the spread of *Ailanthus* can be optimized.

2. Methods

2.1. Site description, harvest and prescribed fire history

This study is located within THSF, the third largest state forest in Ohio, covering 6618 ha (16,354 acres). It lies within the Southern Unglaciated Allegheny Plateau, and the topography is dissected, consisting of sharp ridges, steep slopes, and narrow valleys (Beatley and Bartley, 1959). The uplands consist of mixed-oak overstory and the lower slopes and coves are a mixed mesophytic (Braun, 1950). After European settlement in the early 1800s, this landscape like many in the region, had a history of timber harvesting and farming. By the 1930s, the land had become severely eroded and unproductive. A federal resettlement program relocated subsistence farming families from the area to more productive land and subsequently transferred management to the Ohio Department of Natural Resources (ODNR) Division of Forestry. Today THSF is almost completely forested and has had an active timber harvesting program, a component of its multiple-use management, for more than 50 years. Use of prescribed fire as a management tool began in 2001. Since the 1970s, wildfire has been infrequent and insignificant within THSF (John Stauffer, retired Ohio Division of Forestry District Fire Manager, personal communication May 2017). Recent USDA Forest Service Forest Inventory and Analysis (FIA) data (2007–2011) from a five-county area that includes THSF showed that *Ailanthus* occurred in 5% of 162 FIA plots (Forest Inventory and Analysis Database, 2017). Based on tree coring of several large *Ailanthus* found near roadsides at THSF, we estimated establishment occurred between 1924 and 1936 (Rebbeck, unpublished).

We focused sampling within a 4000-ha block of the forest which provided a mixture of prescribed burned and unburned stands. Approximately 25% of the study area had dormant season prescribed fires between 2001 and 2008 (Fig. 1) within mature mixed oak saw timber stands with slopes ranging from 20 to 60%. The twelve prescribed burns occurred during the dormant season with four in the fall (2001, 2003, 2004, and 2008) and eight in early spring (2001–2003, and 2005–2007). The average size of the units was 105 ha and ranged from 28.4 to 321 ha. Quantitative data related to fire severity was not available for the majority of burn units. Antidotal observations indicate that none of the burns were stand-replacing.

Digital ArcGIS records of timber harvests from 2005 to 2009 and prescribed burns from 2001 to 2008 was provided by the Ohio Division of Forestry. Paper records of timber harvests at THSF prior to 2005 were digitally scanned, and polygons of harvested areas were manually created within ESRI ArcGIS (Version 10, Redlands, CA). A georeferenced database of harvest history was created which included the following attributes for each polygon: harvest year, acres, volume removed, and a harvest type code (broadly defined from the records as no harvest activity, cutting activity as either single or multiple thinning, or clear cut). Incomplete or questionable timber harvest records were resolved with ground surveys. Records indicate that 80% of the study area had previous some harvesting activity (Fig. 1).

2.2. Plot sampling

To document the general forest structure and composition and the abundance of *Ailanthus* across the study area, we established 267 study plots arrayed in a systematic grid (400-m spacing; Fig. 1) in late winter 2009. Field data were collected at each plot in summer 2009. *Ailanthus* absence or presence was recorded within the 40-m radius plot. The diameter at breast height (dbh) and mortal status of *Ailanthus* trees (≥10 cm dbh) were recorded

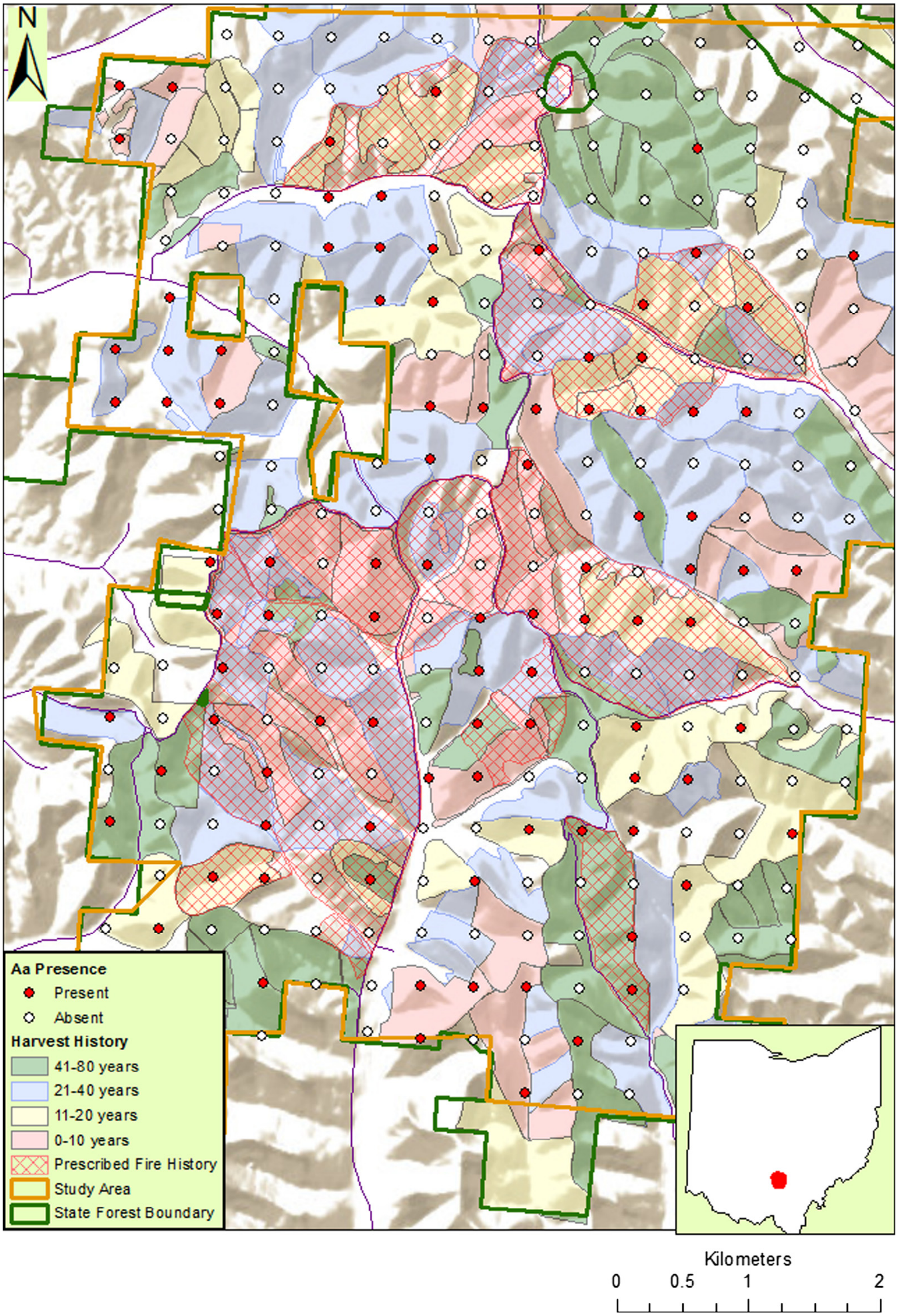
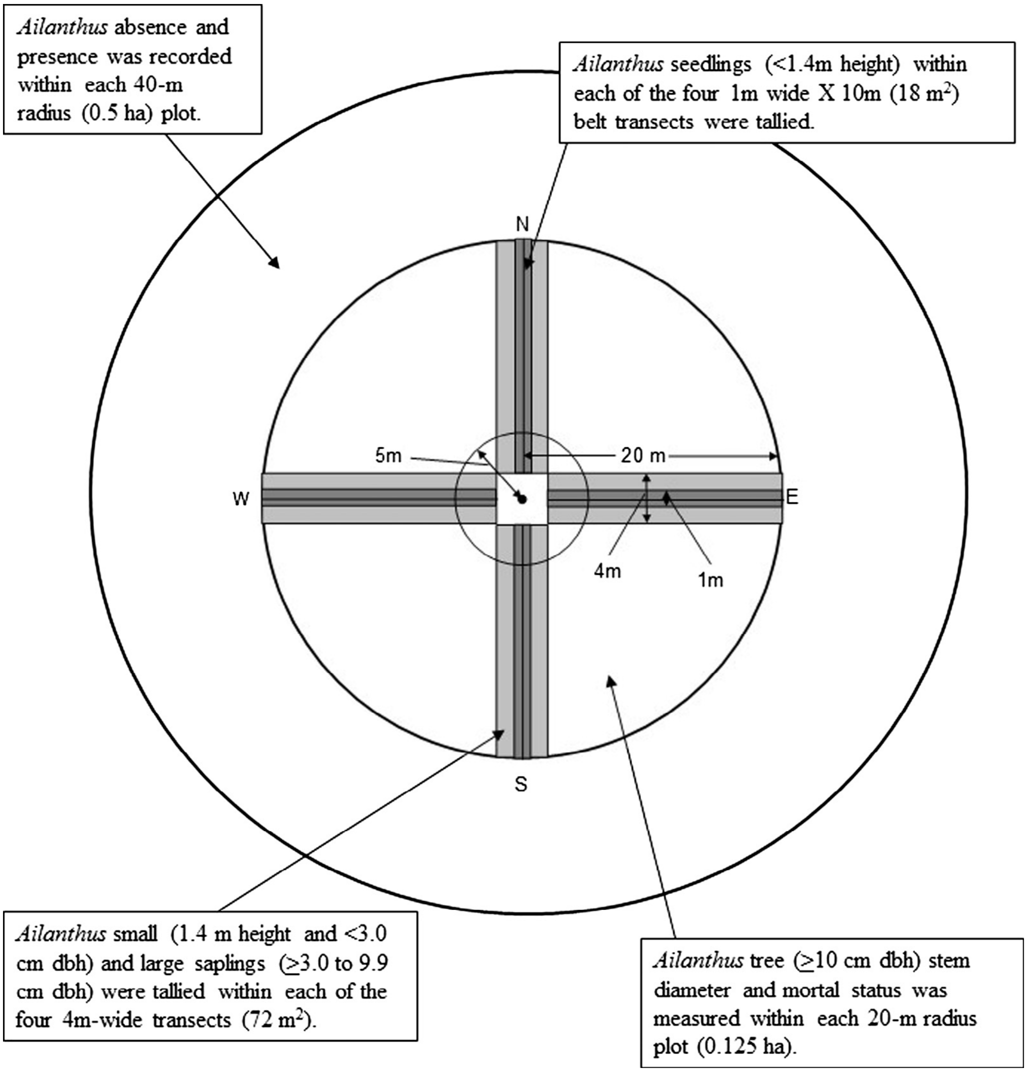


Fig. 1. Plot distribution, harvesting history and prescribed burn history within the 3885-ha study area in Tar Hollow State Forest in southeastern Ohio.

in a 20-m radius circular plot (0.125 ha) at plot center (Fig. 2). In a 4-m wide belt transect (72 m^2 each) located within each 20-m radius subplot, dbh of *Ailanthus* saplings to include small ($\geq$1.4 m tall and <3.0 cm dbh) and large ($\geq$2.9 to <10 cm dbh) was recorded. In addition, all *Ailanthus* seedlings (germinants, true seedlings, and seedling sprouts) <1.4 m in height were counted within four cardinal direction belt transects (each 1-m wide × 18-m long (18 m^2) emanating 2 m from plot center (Fig. 2). Within a 5-m subplot centered in the 20-m radius plot, all large non-*Ailanthus* saplings (3–9.9 cm dbh) were tallied. Basal area (BA) and species composition of overstory trees were estimated from the plot center using a 10-factor (2.3 m^2 ha^{-1} or 10 ft^2 ac^{-1}) basal area prism.

Fire severity, modified from Brose and VanLear (1998), was assessed for each plot while collecting vegetation data. Plots were placed into one of three classes (no burn, very low + low, medium + high) based on a plot average of topkill/mortality of saplings (3–



Ailanthus absence and presence was recorded within each 40-m radius (0.5 ha) plot.

Ailanthus seedlings (<1.4m height) within each of the four 1m wide X 10m (18 m^2) belt transects were tallied.

Ailanthus small (1.4 m height and <3.0 cm dbh) and large saplings (≥3.0 to 9.9 cm dbh) were tallied within each of the four 4m-wide transects (72 m^2).

Ailanthus tree (≥10 cm dbh) stem diameter and mortal status was measured within each 20-m radius plot (0.125 ha).

Fig. 2. Diagram of sampling scheme using to determine absence-presence *Ailanthus* demographics within each 20-m radius plot. In addition, overstory basal area was measured with a 10 factor prism at plot center.

10 cm dbh), midstory (10.1–25.5 cm dbh) injury, topkill or mortality of midstory trees, and bark scorch. Plots outside of prescribed burn units were assigned a non-burn class representing 70% of the plots.

In summer 2009, photosynthetically active radiation (PAR) was measured in each plot with an AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, WA). A separate PAR measurement (1 m height) was taken at plot center and at 5, 10 and 15 m along four 20-m transects (four cardinal directions). A second ceptometer was placed in a nearby clearing to record PAR in full sunlight so that the PAR measured in each plot could be expressed as the percentage of full sunlight. The 13 measurements per plot were averaged for analyses.

2.3. Dendrochronological sampling and Ailanthus establishment dates

Tree cores from *Ailanthus* were collected across the study area to investigate the relationship between *Ailanthus* establishment and timber harvests. Two core samples were collected from 39 randomly selected plots where Ailanthus was found during grid plot sampling and from eight large seed-bearing *Ailanthus* females identified with aerial mapping (Rebbeck et al., 2015). An increment borer was used to collect tree cores at dbh height; however if the tree dbh was smaller than 8 cm dbh, a tree cross-section was collected. Following collection, increment cores were glued onto wooden core mounts and dried. Cross-section samples were surfaced with a power planer. All samples were sanded with series of increasingly fine grit sand paper prior to dating. Establishment date and tree age was then collected from each sample following typical dendrochronology methods (Stokes and Smiley, 1968). Graphical ('skeleton') plots that highlight years of abnormally low tree growth were constructed and then used to cross-date samples against a regional master oak chronology (McEwan et al., 2007). A total of 87 *Ailanthus* trees ranging in size from 3.6 to 43.2 cm dbh were sampled, and establishment dates were estimated. Seven trees where tree-ring series could not be confidently cross-dated were excluded from further analyses. The establishment date of each cored tree was paired with its georeferenced timber harvest record to calculate the year it originated relative to harvest year on record. Sampling locations were equally distributed between burned and unburned areas. The majority of samples were collected within thinned harvest areas dominated by select cuts (73%), 16% were within clear cuts, and 11% were within uncut areas (no evidence of harvesting in the last 80 years).

2.4. Statistical analyses

Stem counts were grouped into two size classes for statistical analyses either "seedlings" which included germinants, true seedlings, seedling sprouts and small saplings (>1.4m tall and <3.0 cm dbh) or "trees" which included all *Ailanthus* stems $\geq$3.0 cm dbh. Presence of *Ailanthus* seedlings and trees were analyzed separately using SAS GLMMIX (Littell et al., 2006) using a multinomial distribution with the cumulative logit link function. Independent variables tested included: (1) fire severity (categorical data: 0 = no burn; 1 = very low + low; 2 = medium + high); (2) years since last burn (categorical data: 0 = no burn, 1 = >20 years, 2 = 8–20 years, 3 = 3–7 years, and 4 = 0–2 years); (3) years since last harvest (categorical data: 1 = 41–80 years, 2 = 21–40 years, 3 = 11–20 years, and 4 = 0–10 years); (4) photosynthetically active radiation (PAR); and (5) aspect index. Aspect index is a continuous variable based on a transformation of aspect (Beers et al., 1966) with values ranging from 0 (NE aspect, 22.5°, typically cool and wet) to 2 (SW aspect, 202.5°, typically warm and dry). Because the data sets contain numerous zeros, the following seedling density classes were created: low (0–100 seedlings ha^{-1}), medium (101–500 seedlings ha^{-1}), and high (>500 seedlings ha^{-1}). Likewise, tree density classes were: low (0–10 stems ha^{-1}), medium (11–50 stems ha^{-1}), and high (51–500 stems ha^{-1}). Density categorical data were analyzed using a multinomial logistic regression approach. Normality of the density class data was accessed using the Shapiro-Wilk test after first testing the lognormal (with the identity link function). Gamma distribution with the log link function best fit the seedling and tree data sets. Residuals from all models were assessed for normality by plotting, and fixed effects were evaluated for homogeneous variance using Levene's test (Brown and Forsythe, 1974). Orthogonal contrasts were run to test the relationship between *Ailanthus* presence and density to timing of harvest activity.

3. Results

3.1. Overstory composition, Ailanthus presence and density

Tree basal area (BA) for all species averaged 24.7 ± 8.6 m^2 ha^{-1} (107.6 ± 37.5 ft^2 ac^{-1}) across the study area, while *Ailanthus* represented <1% of BA. Oaks and hickories represented 37.5% of the BA while other shade-intolerant species such as yellow-poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), and sassafras (*Sassafras albidum*) represented 35.5%. Shade-tolerant species such as red and sugar maple (*Acer rubrum* and *A. saccharum*) represented 25% of the BA.

Table 2
Results of multinomial (ordered) link function cumulative logit models for effects of prescribed fire and harvest history, and aspect on presence and density of *Ailanthus* seedlings (>1.4 m–2.9 cm dbh) and *Ailanthus* trees ($\geq$3.0 cm dbh), and a summary of orthogonal contrasts to time of harvest on presence.

Ailanthus presence		Seedlings		Trees	
Effect	df	Presence	Density	Presence	Density
p values					
Fire	2	0.461	0.079	0.3641	0.651
Harvest activity	3	0.001	0.008	0.0063	0.032
Aspect index	1	0.003	0.955	0.9920	0.691
PAR	1	0.204	0.044	0.496	0.607
Contrasts			Presence		
Time since harvest			Seedling		Trees
p-values					
0–10 vs. 11–20 years			0.957		0.067
0–10 vs. 21–40 years			0.047		0.868
0–10 vs. 41–80 years			<0.001		0.069
11–20 vs. 21–40 years			0.045		0.034
11–20 vs. 41–80 years			<0.001		0.001
21–40 vs. 41–80 years			0.017		0.076

Both *Ailanthus* seedling and tree densities were generally low across the entire forested landscape. *Ailanthus* seedlings were present in 35% of the plots while trees were present in 17% of the plots. *Ailanthus* tree densities were either zero or low (0–10 stems ha^{-1}) in 86% of the plots. The mean density of *Ailanthus* seedlings across the study area was 282.3 ± 93.8 stems ha^{-1} with a maximum of 21,285 stems ha^{-1}. The mean density of *Ailanthus* trees was 21.4 ± 8.7 stems ha^{-1} with a maximum of 2193 stems ha^{-1} on one plot (all others had <500 stems ha^{-1}). High densities of both seedlings (>500 seedlings ha^{-1}) and trees (51–500 stems ha^{-1}) were observed in <10% of the plots. Of the 80 plots (30% of total) that did have observed fire activity, 71% were rated as very low to low fire intensity and 29% were rated as medium to high fire intensity. Plots were evenly distributed across areas with four different time classes of timber harvesting activity. The type of harvest activity varied over the last 80 years; approximately 21% of the plots had no harvest activity; 58% had one thinning activity; 10% had multiple thinnings; and 11% had been clear cut. Medium and high densities of *Ailanthus* seedlings were found within areas that had been harvested within the last 20 years, 2.3 times as much as those that been harvested 21–80 years ago (Table 1).

Based on the multinomial logit models, prescribed fire was not a significant predictor of *Ailanthus* either presence or density in any

Table 1
Frequency distribution (number of plots and % of plots) of *Ailanthus* seedling and tree density associated with years since last timber harvest activity in 267 grid point plots across 3885 ha study area within Tar Hollow State Forest located within southeastern Ohio, USA.

Ailanthus stem density	Years from last harvest and number of plots							
	0–10 yrs (N = 61)		11–20 yrs (N = 58)		21–40 yrs (N = 73)		41–80 yrs[a] (N = 75)	
	#	%	#	%	#	%	#	%
Seedlings								
None (0 seedlings ha^{-1})	36	59	41	71	60	82	70	93
Low (1–100 seedlings ha^{-1})	5	8	2	3	2	3	1	1
Medium (101–500 seedlings ha^{-1})	10	16.5	10	17	6	8	1	1
High (>500 seedlings ha^{-1})	10	16.5	5	9	5	7	3	4
Trees								
None (0 stems ha^{-1})	51	84	39	67	62	85	70	93
Low (1–10 stems ha^{-1})	0	0	4	7	3	4	0	0
Medium (11–50 stems ha^{-1})	4	6	5	9	4	5.5	2	3
High (51–>500 stems ha^{-1})	6	10	10	17	4	5.5	3	4

[a] Plots with no harvest activity were assigned a default date of 80 years since last harvest since that represents the time of public land acquisition. Of the 75 grid point plots that fell within the 41–80 years harvest activity class, 55 (73%) had no record of past harvest activity and no signs of past timbering activity during ground surveys.

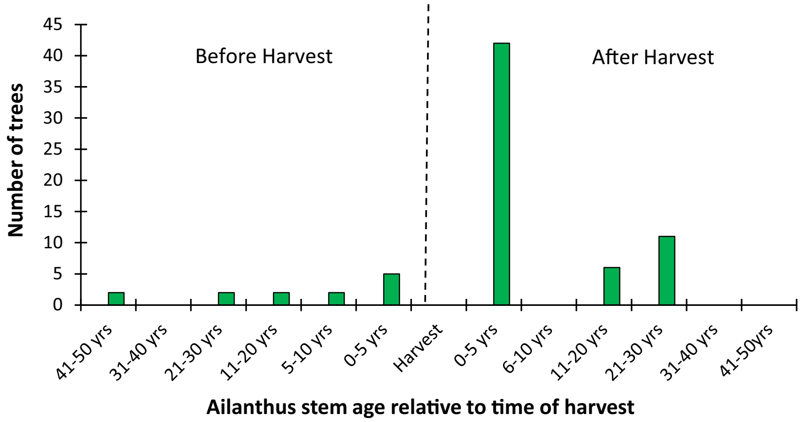


Fig. 3. Association of *Ailanthus* establishment and harvest history within the 3885-ha study area. Dendrochronological analyses were conducted on 87 tree cores collected from stands with differing timber harvesting histories from 1930 until 2010. Collection sites were equally represented in burned and unburned areas.

of the models tested (Table 2). Timber harvest activity was the best predictor of *Ailanthus* presence (seedlings, $p = 0.001$; trees, $p = 0.006$) and density (seedlings, $p = 0.008$; trees, $p = 0.032$). Results of orthogonal contrasts demonstrated that *Ailanthus* seedling presence was more likely in areas harvested within 0–10 years, 11–20 years, or 21–40 years compared with older harvests (41–80 years) (Table 2). Similarly orthogonal contrasts showed that predicting tree presence was more likely in areas harvested within 11–20 years than those harvested 41–80 years. Aspect index (AI) was a significant predictor for *Ailanthus* seedling presence ($p = 0.003$) but not for tree presence and not for seedling or tree density. Of the plots where seedlings were found, 58% had AI ranging from 0 to 1 (indicative of cooler, moister sites), while 42% of the plots had AI ranging from 1 to 2 (indicative of warmer, drier sites). In plots where seedlings were absent, 43% had AI ranging from 0 to 1 and 57% had AI ranging from 1 to 2. Percentage of full sun (PAR) was a significant predictor of *Ailanthus* seedling density ($p = 0.044$) but not of seedling presence. *Ailanthus* seedling density increased with increasing PAR: 4.2% of full sun for plots with low densities (0–100 seedlings ha^{-1}) compared with 12.7% of full sun for plots with high densities (>500 seedlings ha^{-1}). *Ailanthus* tree presence and density were not predicted by either aspect index or PAR. Across the entire study area, PAR measured at 1 m above forest floor averaged 5.6% of full sun with 72% of the plots at levels $\leq$5% of full sunlight.

3.2. Ailanthus establishment in relation to timber harvesting

Harvest history and time of *Ailanthus* establishment was verified with 87 cored *Ailanthus* trees. Of the trees cored, 72 (83%) were in stands that had been timber harvested. Tree age ranged from 5 to 76 years old. We found that 54% of the trees sampled originated 1–3 years after a timber harvest (Fig. 3).

4. Discussion

We capitalized on a unique opportunity to investigate the effects of forest management activities on *Ailanthus* demography in a topographically dissected forested landscape within southeastern Ohio. We had access to both historical paper and digital georeferenced timber management records dating back to the 1930s. In addition, almost a quarter of the 3885-ha study area had been prescribed-burned between 2001 and 2008. This landscape has had a long history of timber harvesting and subsistence farming since the early 1800s. Past land use likely facilitated the establishment of the current *Ailanthus* populations across the study area as it reverted back to forest in the 1930s. *Ailanthus* became popular in small cities and towns across New England and Mid-Atlantic regions in the mid-1850s (Kasson et al., 2013) which likely contributed to its subsequent spread into smaller farming communities. *Ailanthus* are actually longer-lived than the often cited 30–50 years (Miller, 1990). Kasson et al. (2013) conducted tree-ring analyses on *Ailanthus* samples from Pennsylvania, Delaware, New York, Ohio, Virginia, and West Virginia and found that reaching ages of more than 100 years, with females still producing viable seeds. In earlier dendrochronological sampling, we found that *Ailanthus* had been present on the THSF landscape for at least 85 years (Rebbeck, unpublished).

Although *Ailanthus* represented less than 1% of the total basal area, *Ailanthus* trees were present on 17% of the plots, most often at densities of 0–10 stems ha^{-1} (86%). However, 9% of plots had higher tree densities of 51–500 stems ha^{-1} and one outlier plot had 2193 stems ha^{-1}. This outlier plot fell within an intensively harvested area that had been clear cut in 1974 followed by a select cut harvest 22 years later. Mapping these high density areas is a crucial initial step to minimize future spread through explosive growth, given its aggressive clonal nature and high fecundity. Not surprising, the presence of seedlings was twice as common as trees. These demographic distributions have been previously observed for *Ailanthus* within the Central Appalachian region (Call and Nilsen, 2003). As seen with the spatial distribution of tree densities across THSF, a small proportion of the plots (9%) had seedling densities exceeding 500 seedlings ha^{-1}. These observed seedling and sapling densities are similar to those reported by Carter and Fredericksen (2007) in south central Virginia forests and exceed those reported by Kowarik (1995) in West Virginia. These patterns suggest that *Ailanthus* populations exploited canopy openings resulting from disturbances and are presently poised to capitalize future gaps resulting from harvesting, prescribed fire, extreme weather events, or biotic agents.

It is not surprising, given the distribution of *Ailanthus* across this actively managed forest landscape, that harvest activity was the best predictor of the presence and density of both seedlings and trees. A history of recent prescribed fire was not a statistically significant predictor of either presence or density of seedlings and trees. It is also likely that the effects of previous wildfires on *Ailanthus* distributions were insignificant, because fire occurred infrequently and were kept small by suppression efforts, at least since the 1970s (John Stauffer, retired Ohio Division of Forestry District Manager, personal communication, May 2017). In general, fire control, which began in southern Ohio in 1923, greatly reduced the acres of forest that were burned annually (Leete, 1938). Since most of the sites have had some past harvest activity, it is difficult to discern how prescribed fire may have acted alone. In addition, seed-producing females, found while conducting aerial surveys to assist with the current study (Rebbeck et al., 2015), were abundant within harvested areas thus increasing the potential for more establishment via seed dispersal within harvested areas.

Aspect index, a continuous (0–2) variable based on a transformation of aspect, was a significant predictor of seedling presence. A higher proportion of plots with seedlings present were on cooler and moister sites compared with plots absent of seedlings, which tended to be warmer and drier. A similar association pattern of Ailanthus regeneration to aspect was observed in low elevation abandoned chestnut orchards and coppice forests in southern Switzerland (Knüsel et al., 2017). Huebner and Tobin (2006) found that hardwood forests located on northeast-facing slopes, on more mesic conditions, or in 15-year-old clear cuts were more likely to be invaded by non-native plants. They found that invasion into clear cut sites was more dependent on the microsite conditions compared with invasion into mature forests, which were more dependent on surrounding landscape features such as proximity to roads. Kota et al. (2007) reported higher rates of *Ailanthus* seed germination after 2 years in north-facing clear cuts compared to south-facing sites because a greater number of moist microsites favorable for germination and seedling establishment were created after harvesting, albeit temporary.

Percentage of full sun (PAR) was a significant predictor only for seedling density. Plots with low seedling densities were shadier (4% full sun) compared to plots with high seedling densities (13% full sun). Typically, newly-germinated *Ailanthus* seedlings do not persist in shaded environments beyond 1 year (Kowarik, 1995; Knapp and Canham, 2000). However, Knüsel et al. (2017) reported that seed-borne and young clonal ramets of *Ailanthus* were able to grow and survive in low light conditions for up to 7 years. They proposed reclassifying *Ailanthus* as a low to intermediate shade tolerant species during its early regeneration phase. Clearly additional studies are needed to determine the shade tolerance of *Ailanthus* in its early life stages.

Average light levels (percent of full sun) measured during demographic sampling were higher in plots within burned areas (9% of full sun) compared to plots in unburned areas (4% of full sun). These light levels are not reflective of the light conditions that were present at the critical time of *Ailanthus* establishment immediately after prescribed fires or harvesting treatments but do provide some insight. Although these higher light conditions may have favored the growth of *Ailanthus*, it is likely that other species may have responded positively as well, possibly out-competing *Ailanthus* seedlings. Martin et al. (2010) reported that growth rates of five native tree species growing in closed canopy-forests in low light (<3% full sun) in Connecticut, USA exceeded that of *Ailanthus*. They also found that *Ailanthus* mortality was high at 10% full sun, exceeding that of all native species.

Although available light is an important driver for initial *Ailanthus* seedling establishment, is not crucial for clonal growth and establishment. Kowarik (1995) presented three pathways of persistence for light-demanding species in a closed forests: banking of seeds, seedlings, and clonal ramets. He suggested that *Ailanthus* can utilize both seed and ramet banking. Current literature indicates that seeds do not remain viable beyond 2 years (Kota et al., 2007; Kowarik and Säumel, 2007). Given its aggressive sprouting, ramet banking remains the most viable pathway in shady environments because shaded clones can share assimilates with other clones growing in sunnier locations (Kowarik, 1995; Knapp and Canham, 2000). With higher light levels, *Ailanthus* appears to be competitive with most native associates.

A greater proportion of plots in areas harvested within the past 20 years had seedlings and trees present, and at higher densities, than plots in areas harvested either 21–40 years or 41–80 years ago. Knapp and Canham (2000) demonstrated that clonal *Ailanthus* can remain suppressed in shaded forest conditions for >20 years until a gap is created. They compared *Ailanthus* to yellow-poplar, a gap-obligate for recruitment into the forest canopy that depends not on shade-tolerance but on rapid growth to canopy height during a single period of release. This is a viable explanation as to how *Ailanthus* can quickly occupy highly disturbed sites after a timber harvest. Our tree coring data showed that 54% of the sampled *Ailanthus* trees established within 0–3 years of a timber harvest. Call and Nilsen (2003) reported that *Ailanthus* exhibits a preference for establishing in heavily disturbed and compacted areas within shelterwood areas, with a particular affinity to skid trail invasions. Carter and Fredericksen (2007) also found that recent logging appears to promote the colonization of *Ailanthus,* and that the density of *Ailanthus* seedlings and saplings on recently logged mature forests in south-central Virginia are only surpassed by yellow-poplar.

The ability of non-native plants to invade a particular forest depends on the growth characteristics of the species and the scale of the disturbance (Runkle, 1985). Although dormant-season low-intensity prescribed fire alone is a disturbance that can facilitate the establishment of *Ailanthus* and other non-native invasives within eastern United States forests, post-prescribed fire invasions are likely less severe than those after timber harvests. Typically harvesting causes more soil disturbance than prescribed fires. Even though soil-disturbing equipment such as dozers are often used to install fire breaks, the area impacted is minimal when compared with conventional timber harvests, which require the installment of skid and logging trails as well as logging yards. Information available regarding the response of invasive species to wildfire is limited primarily to observation-based anecdotes with few empirical studies in the United States (Gucker et al., 2012). Kuppinger et al. (2010) studied the invasion and persistence of another woody non-native, princess tree (*Paulownia tomentosa*) in the southern Appalachian Mountains of North America and found that its presence was most strongly related to residual vegetation cover, topographic shading, and moisture availability six years after high intensity wildfires.

Seasonality and fire severity are important modulators of the potential disturbance effects of fire in eastern U.S. forests. In our study, all prescribed burns were single fires with the exception of one unit; burns were implemented during the dormant season, with four in the fall and eight in the early spring. In eastern United States hardwood forests, spring and summer fires cause the greatest reduction in woody stem densities compared with dormant season fires (Brose and VanLear, 1998). Most of the burns scored as very low to low fire intensity (81%), while a small portion were medium to high intensity fires (9%) based on vegetation responses during demographic data collections. No overstory mortality associated with burning was observed. Likely these fires consumed leaf litter, exposing patches of bare mineral soil and promoting increased soil surface temperature and nutrients, thereby improving seed bed conditions for *Ailanthus* and native species such as yellow-poplar. This can coincide with the release of a pulse of native shade-intolerant germinants from the seed bank that often occurs immediately after a fire; their growth may be short-lived, however, because they cannot persist under closed canopies (Iverson et al., 2008). *Ailanthus* seedling mortality typically occurs within 1 year under intact forest canopies (Forgione, 1993; Kowarik, 1995; Knapp and Canham, 2000). Manipulative field studies assessing the direct impacts of prescribed fire on *Ailanthus* are needed to refine effective control strategies.

5. Conclusions and management recommendations

Despite the limitation imposed by a single, though large and diverse, study area, our findings do provide empirical data to validate anecdotal observations made by forest managers regarding disturbances associated with timber harvesting; they do not, however, support observations from others related to increases in *Ailanthus* invasions associated with prescribed burning in eastern U.S. hardwood forests. Although overall *Ailanthus* density across the 3885-ha landscape was low, scattered populations were present, and some of these were high density populations mixed with heavy seed-producing *Ailanthus*. These populations are poised for rapid growth through clonal sprouting or abundant seed dispersal with continued human-induced disturbances such as timber harvesting or from natural disturbances associated with extreme weather events or unforeseen biotic agents. Kasson et al. (2013) reported recent widespread *Ailanthus* invasions in Pennsylvania forests following salvage cutting in the aftermath of extensive gypsy moth (*Lymantria dispar*) outbreaks. *Ailanthus* also invaded canopy gaps resulting from *Tsuga canadensis* mortality in stands infested with hemlock woolly adelgid (*Adelges tsugae*) (Orwig and Foster, 1998). As emerald ash borer (EAB) spreads across the eastern United States (EAB Network, 2015), the demise of *Fraxinus* species in these forests may create vast areas vulnerable to invasive non-native plants, which could include *Ailanthus* (Gandhi and Herms, 2010). As second-growth forests mature, timber harvests are on the increase. With additional disturbances, areas infested with *Ailanthus* will continue to increase. Being proactive and reducing/minimizing dispersal of *Ailanthus* is crucial to slow its spread. We are utilizing these findings to develop a habitat suitability index for *Ailanthus* that may serve to identify areas across forested landscapes that have a higher probability of invasion by *Ailanthus*. Preventing *Ailanthus* and other non-native invasive plants from establishing in disturbed sites (e.g., harvested and burned areas) is the most effective and least costly management method. This can be accomplished through early detection and eradication, particularly of seed-producing females (which should be a high priority), careful monitoring and follow-up, and limiting dispersal of invasive plant propagules into burned areas.

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