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How long do seeds of the invasive tree, *Ailanthus altissima* remain viable?

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ABSTRACT

The non-native invasive tree, *Ailanthus altissima* is an increasing threat to the diversity and health of temperate forests. Female trees are prolific producers of wind-dispersed seeds. It is not known if *Ailanthus* seeds remain viable in natural growing conditions beyond two years. We collected *Ailanthus* seeds from eleven sources in fall 2010 and incubated outdoors in either mixed oak leaf litter or mineral soil (10 cm depth) for five years to assess seed viability. Each May sets of seeds were retrieved, counted and sown in a greenhouse to measure germination. Initially germination rates averaged 87%, however in year 5 (2016), germination rates of seeds incubated outdoors in oak leaf litter, fell to 1.9%, while those incubated in mineral soil averaged 75%. Germination rates of soil-incubated seeds ranged from 48 to 95% among the eleven seed sources after five years. These findings demonstrate that the common practice to eliminate *Ailanthus* seed sources two years prior to a timber harvest is insufficient to deplete its seed bank. We propose that managers remove seed sources at minimum of six years in advance of a scheduled timber harvest. Ideally, it would be most advantageous to incorporate removal of females *Ailanthus* as a routine management practice.

1. Introduction

Native to northeastern China, *Ailanthus altissima* (*Ailanthus*, tree-of-heaven, Chinese sumac, stink tree), is widely distributed throughout many temperate regions of the world including all continents with the exception of Antarctica (Kowarik and Säumel, 2007). It has been present in North American landscapes since being introduced into Philadelphia, PA USA in 1784 (Kasson et al., 2013). *Ailanthus* is often considered a forest edge species, but its presence within interior forest sites is common (Ellenwood et al., 2015; Rebbeck et al., 2017). It is fast growing, reaching heights of 18–21 m in 10 years (Knapp and Canham, 2000; Kowarik and Säumel, 2007). *Ailanthus*'s tendency of aggressive clonal spread, creates dense thickets which can out-compete native trees, increasing its infamous invasive potential.

This dioecious tree is a prolific seeder with average annual seed production estimates of 325,000 per tree (Bory and Clair-Maczulajtys, 1980). Wickert et al. (2017) reported seed production is positively related to tree diameter, with *Ailanthus* trees exceeding 20 cm dbh capable of producing > 1 million seeds in a single year. Seeds are found singly in oblong, papery thin, 33–48 mm long spirally-twisted samaras lacking endosperm (Zasada and Little, 2008). Seeds develop as numerous dense clusters in the summer, mature in early fall and typically persist on the tree until spring. Wind-dispersed seeds can travel in excess of 200 m (Landenberger et al., 2007) with the potential of invading newly disturbed sites. Secondary dispersal is common on the ground as well as along streams and rivers (Säumel and Kowarik, 2010).

Few experimental studies have monitored native seed survival viability in forested ecosystems (Marquis, 1975, Granström, 1987). Clark and Boyce (1964) found yellow-poplar, *Liriodendron tulipifera* seeds, a native species with a similar life history and ecological niche to *Ailanthus* remained viable for four years under forest litter. Globally, non-native invasive species often have large and persistent seed banks (D'Antonio and Meyerson, 2002). However, North American studies on the seed bank persistence and viability of non-native woody plant species have been limited primarily to herbaceous non-natives (Blaney and Kotanen, 2001; Huebner, 2011). The persistence of *Ailanthus* seeds in soil seed banks has not been studied beyond two years (Kowarik and Säumel, 2007). Seeds do not appear to require stratification to germinate, but germination rates can increase to 96% following cold stratification (Graves, 1990). *Ailanthus* seeds are not dependent on high light conditions for germination and can germinate and persist in closed canopy forests (Kota et al., 2007; Martin et al., 2010). Kaproth and McGraw (2008) reported that *Ailanthus* seeds submerged in water for five months retained high germination rates (94%). These traits verify its potential for high fecundity in unfavorable growing environments. There are many factors that lead to increased *Ailanthus* regeneration including prescribed fire, herbicide use and timber harvesting.

It is important to understand how forest management practices

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influence the dissemination of vegetation and seed propagules of *Ailanthus* and other non-native invasive plants to minimize their human-facilitated spread. We found that timber harvests within 20 years predicted the presence of *Ailanthus* in southeastern Ohio mixed oak forests while recent prescribed burns (≤8 years) did not (Rebbeck et al., 2017). Anecdotally, forest managers in the eastern United States have reported increases in *Ailanthus* seedlings immediately following prescribed fires. It may be that fire, by reducing leaf litter and increasing available light, creates improved conditions for *Ailanthus* seedling establishment as observed for native species such as yellow-poplar (Hutchinson et al., 2005). In addition, herbicide to control interfering vegetation may alter forest floor light conditions and stimulate germination of native and non-native seed banks (Horsley, 1994). Soil disturbances resulting from the use of heavy equipment such as dozers and skidders for timber harvesting and prescribed fire may also facilitate *Ailanthus* seed germination and dispersal of vegetative fragments capable of rooting (Rebbeck et al., 2017).

Understanding the basic biology of non-natives such as *Ailanthus* is crucial to choosing appropriate forest management practices that do not facilitate dispersal. Current proactive control recommendations include the removal of *Ailanthus* seed sources more than 200 m from a planned timber harvest (Landenberger et al., 2007). Unfortunately we do not know how long in advance of a disturbance managers should wait for the *Ailanthus* seed bank to be exhausted because its seed longevity has not been studied beyond two years (Kowarik and Säumel, 2007). Our objective is to determine if *Ailanthus* seeds remain viable when maintained in either forest litter or buried in mineral soil for five years.

2. Methods

2.1. Study design

A repeated measures nested factorial design tested the effect of three factors on the germination of retrieved *Ailanthus* seeds: (1) seed incubation location, either under natural forest leaf litter (soil depth = 0 cm) or burial (soil depth = 10 cm); (2) seed source (11 mother trees from central and southeastern Ohio) and (3) length of incubation (1–5 years). The incubation locations were chosen to simulate two possible seed dispersal scenarios which might occur within forests: (1) where no active management occurred as represented by leaf litter incubations, and (2) within actively managed forests where seeds are buried by harvesting or road-building equipment.

Ailanthus seeds were collected in October 2010. Sites locations of seed trees were georeferenced using a hand-held GARMIN GPSmap 76CSx unit (Table 1). In November 2010, lots of 50 seeds were counted and placed into 20 × 20 cm, 5 mm plastic mesh litter bags for each of the 11 seed sources. The LG10 and LG11 sources had 30 seeds per bag because fewer seeds were collected. Each litter bag was uniquely identified with a metal numbered tag.

The two incubation locations were established at the USDA Forest Service Laboratory, Delaware Ohio (40°21′21″N, 83°03′52″W) in early November 2010. Seeds were incubated in either a closed canopy 50 year-old hardwood stand dominated by northern red oak (*Quercus rubra* L.) stems (30–40 cm dbh) or within a nearby (< 100 m) open and regularly mowed area. Both areas were underlain by Morley silt loam found on till plains and moraines of Wisconsin age in glaciated regions of Ohio. Within the hardwood stand, three rows of six 50 × 50 cm incubation plots each were setup within a 20 × 50 m area as complete replicates for leaf litter incubations. Each plot contained a 20 × 20 cm seed bag folded in half with 50 seeds from each of the 11 seed sources which were randomly positioned within each plot. Litter bags were secured to the forest floor or soil with steel pins and then covered with anchored 12 × 24-mm opening hardware cloth to minimize disturbance by wildlife. Leaf litter depth within the site averaged 3 cm.

A duplicate set of seeds were buried to a depth of 10 cm within 18 50 × 50-cm plots within a mowed turf grass area immediately west of a 15-year-old yellow-poplar plantation. This area was cleared of grass and rototilled to a depth of 15 cm. To minimize seed loss and improve seed bag retrieval, a single layer of fiberglass mesh window screen was placed between the bare soil and the seed bags. Soil was placed over the hardware anchored seed bags to a depth of 10 cm, then burial locations were covered with oak leaf litter collected from the hardwood stand to a depth that simulated annual leaf litter deposition. To minimize wind displacement of oak leaf litter, plots were covered with anchored plastic deer-fence. Each autumn, fresh oak leaf litter was added to the buried seed plots. Each seed source by time of incubation combination was replicated three times at the two seed incubation locations. A total of 396 L bags (11 seed sources × 6 collections × 3 replicates × 2 incubation locations) holding a total of 18,360 seeds were deployed.

Hourly air and bare soil (5 cm depth) temperatures were collected at an onsite weather station, cooperatively managed by USDA Forest Service, Delaware, OH and Ohio Agricultural Research and Development Center, The Ohio State University, Wooster, OH. Soil (10-cm depth) and air temperatures were also monitored hourly using an Onset HOBO thermocouple probe/datalogger within the center of the hardwood plantation incubation site.

The daily mean air and soil temperatures recorded at the weather station are summarized in Fig. 1. Monthly air and bare soil temperatures at 5 cm averaged −0.35 °C and 1.45 °C in January, respectively and 23 °C and 25 °C in July, respectively during the study. Because of intermittent equipment failures, temperature data was missing from January 26, 2011 to May 30, 2011, February 8, 2012 to March 2012 and July 9, 2013 to June 5, 2014. Rainfall data were collected onsite at the National Atmospheric Deposition Program National Trends Network OH17 Site station (NADP National Trends Network 2018). Annual mean rainfall was 1111 mm from 2011 to 2016. The highest observed annual precipitation of 1445 mm was measured in 2011, while the lowest (951 mm) was measured the following year. June was the wettest month most frequently (≥120 mm rainfall) while November was the driest month (≤50 mm rainfall) observed during the study

Table 1
Locations of 11 seed-bearing *Ailanthus* trees in central and southeastern Ohio and percent seed germination from 2011 to 2016.

Tree ID	Ohio City, County	Latitude, longitude	Seed collection date	Percent germination	Percent germination[a] minimum – maximum
DE01	Delaware, Delaware	40°17′59″N, 83°03′45″W	10/05/2010	46.2 ± 5.5 de	36.4 (2015) – 66.3
DE02	Delaware, Delaware	40°18′01″N, 83°04′59″W	10/24/2010	55.9 ± 5.3bcde	39.0 (2013) – 86.6
DE03	Delaware, Delaware	40°18′02″N, 83°04′01″W	10/24/2010	55.0 ± 5.8 bcde	47.3 (2015) – 79.8
DE04	Delaware, Delaware	40°18′11″N, 83°04′10″W	10/24/2010	66.4 ± 5.7 ab	52.3 (2013) – 95.1
DU05	Dublin, Franklin	40°06′07″N, 83°06′37″W	10/22/2010	63.9 ± 5.5 abc	51.6 (2016) – 87.6
DU06	Dublin, Franklin	40°06′09″N, 83°06′35″W	10/22/2010	56.9 ± 5.4 bcd	49.5 (2014) – 84.4
SB07	South Bloomfield, Pickaway	39°46′22″N, 82°59′22″W	10/23/2010	61.2 ± 5.1 abcd	49.0 (2016) – 85.0
LD08	Londonderry, Ross	39°16′04″N, 82°47′32″W	10/23/2010	70.8 ± 5.5 a	56.8 (2016) – 96.6
LD09	Londonderry, Ross	39°16′06″N, 82°47′24″W	10/23/2010	49.6 ± 5.0 cde	37.4 (2016) – 76.36
LG10	Logan, Hocking	39°32′31″N, 82°25′12″W	10/25/2010	38.8 ± 5.0 e	25.9 (2015) – 56.3
LG11	Logan, Hocking	39°32′04″N, 82°24′47″W	10/25/2010	64.8 ± 6.2 ab	49.7 (2016) – 87.6

[a] Year of observed minimum annual percent germination is shown in parenthesis; maximum values were all observed in 2011.

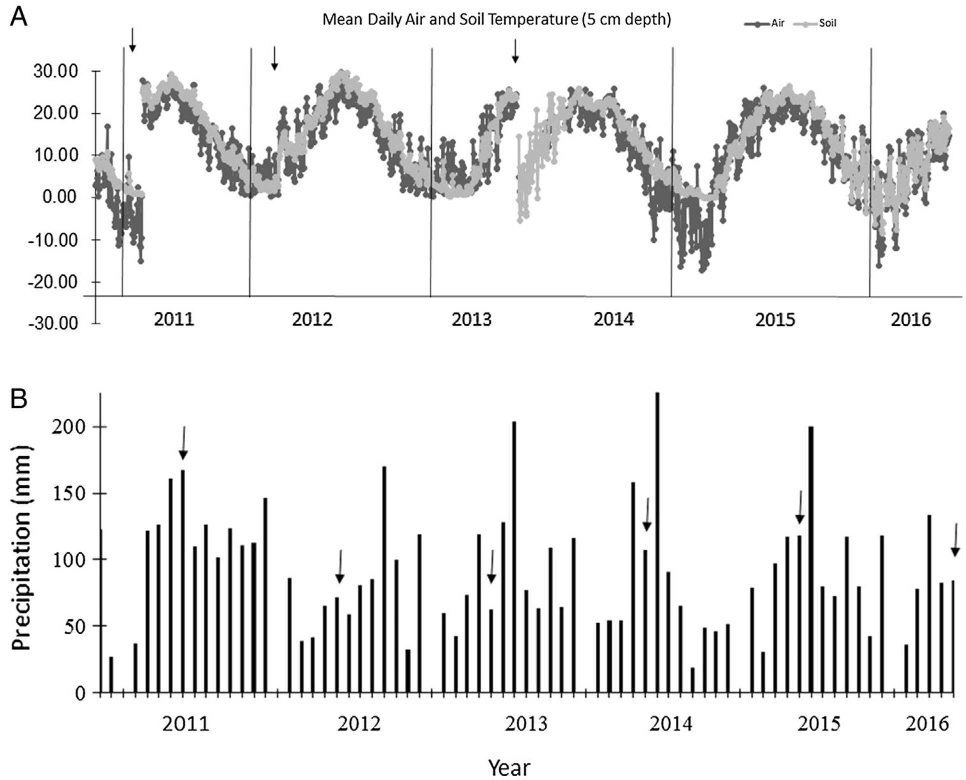

Fig. 1. Summary of environmental conditions during *Ailanthus* seed incubations from Nov. 2010 until May 2016 in Delaware, OH, USA. A. Daily mean temperature. B. Monthly precipitation totals. Dashed arrows indicate time when seed lots were collected from incubation sites for germination trials.

(Fig. 1B).

2.2. Seed germination tests

Annually in mid-May from 2011 to 2016, seed bags were retrieved and seeds were counted then planted in 19.5 × 19.5 × 5.2 cm trays containing Metro Mix 510 soil mix (Sun Gro Horticulture Canada Ltd., Vancouver, NC, Canada) and maintained in a climate controlled greenhouse. Daily air temperatures averaged 26.5 ± 0.4 °C during the germination trials. Seed trays were watered as needed to maintain moist conditions. The number of germinants were counted daily over a 30-day period and used to calculate percent germination for retrieved seeds for each seed source bag replicate.

2.3. Viability of fresh and lab-stored seeds

On November 4, 2010, an additional set of 50 seeds per source (25 seeds for SB07) were stored at 1–4 °C for 88 days to determine the germination of fresh seeds after artificial stratification. In April 2011, these seed trays were transferred to a climate-controlled greenhouse (25 °C day/20 °C night air temp, 12 h daylight) and monitored for germination. In May 2016, an additional greenhouse experiment was run to determine the viability of seeds stored under laboratory conditions for 5½ years. For each of the original seed sources, 50 seeds were planted in soil trays and monitored for germination as previously described, with the exception of SB07 since no seeds remained.

2.4. Statistical analysis

A repeated measures nested factorial design was used to test percent germination of the retrieved seeds per replicate of 50 seeds. The raw percentage data were not normally distributed and were arc sine transformed, a common transformation for germination data (Scott et al., 1984). A linear mixed model (GLMMIX) was employed using SAS 9.4 (SAS Institute Inc., Cary NC, USA). Replication nested within seed source was considered the random effect. To account for the correlation and heterogeneity between years, we used a heterogeneous autoregressive first order covariance structure. Year was treated as a random effect. An alpha level of 0.05 was used to determine significance.

3. Results

3.1. Germination of fresh and lab-stored seeds

Germination of artificially cold-stratified fresh seeds in April 2011 averaged 87 ± 3.3% with rates ranging from 56 to 97% depending on seed source. In 2016, germination averaged 83.5 ± 3.1% for 5 ½-year-old seeds stored under constant laboratory conditions.

3.2. Viability of outdoor incubated seeds

Germination rates of seeds incubated outdoors in either oak leaf litter or mineral soil from November 2010 until mid-May 2016 averaged 48.4 ± 5.5%. *Ailanthus* seed germination was significantly affected by seed source and there was a significant incubation site by year interaction (Table 2). Germination rates of seeds incubated in mineral soil remained fairly constant, ranging from 83% (2011) to 79.4% (2016), while those incubated in leaf litter declined over time from 81% (2011) to 1.9% (2011) (Fig. 2). Seed source affected germination and ranged from 38.8 ± 5.0 to 70.8 ± 5.5% (Table 1).

4. Discussion

Some *Ailanthus* seeds still germinated after five years when incubated in either mixed oak leaf litter or buried in soil at 10 cm. Over the 5 plus years of this study, germination rates of seeds incubated in leaf litter declined rapidly from 81 to 1.9% compared to the more

Table 2
Statistical model results with arc sine transformed percent germination data of *Ailanthus* seeds incubated over 5 years.

Effect	Num DF	Den DF	F value	Pr > F
Seed source	10	57.68	8.77	< 0.0001
Incubation site	1	5.35	152.37	< 0.0001
Seed source * incubation site	10	57.68	0.93	0.5125
Year	5	94.84	79.32	< 0.0001
Seed source * year	50	166.9	0.93	0.6032
Incubation site * year	5	94.84	50.53	< 0.0001
Seed source * incubation site * year	50	166.9	0.72	0.9076

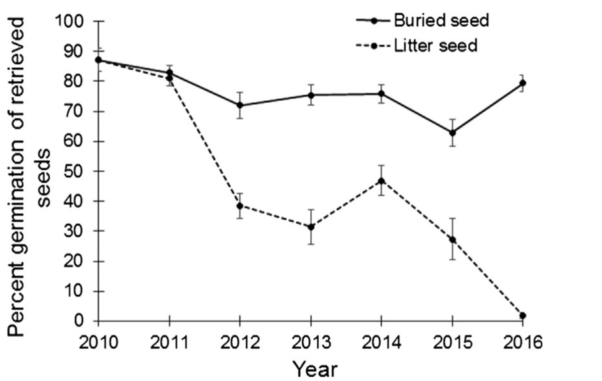

Fig. 2. Mean germination of retrieved *Ailanthus* seeds incubated in either mixed oak leaf litter or buried in mineral soil at 10 cm depth from Nov. 2010 through May 2016.

uniform germination rates of 75% observed for seeds buried in mineral soil. Moisture and temperature conditions within the leaf litter were likely more variable than those observed for the soil-incubated seeds. Accumulated litter modulates the forest floor microenvironment by increasing shade, reducing maximum soil temperatures as well as soil evaporation (Facelli and Pickett, 1991). No efforts were made to maintain evenly distributed leaf litter within the plots located within mixed hardwood stand, whereas a layer of uniform oak leaf litter was maintained to minimize germination of dormant non-*Ailanthus* seeds present in the seed bank after the soil had been tilled for the buried seed plots. During the first seed retrieval (2011) we did observe multiple seeds with emerging radicles where leaf litter cover was shallow in one of the three replicate plots within the hardwood stand as well as one of the soil-buried plots. No signs of germination were observed during subsequent seed bag retrievals. Leaf litter depth was not measured during annual retrievals of the incubated seed bags but we estimated that leaf litter depths averaged 3 cm and two of the 18 plots had sparse cover during the experiment. Kostel-Hughes et al. (2005), however, reported that leaf litter depths ranging from 0 to 5 cm had no significant effect on *Ailanthus* seedling emergence. They suggested that *Ailanthus*'s ability to germinate in a wide range of litter conditions could be an attribute that has contributed to its success as an invasive species. Facelli (1994) also reported similar germination responses within early successional, abandoned old field sites.

Ailanthus seeds have been reported to be sensitive to moisture and fluctuating temperatures, but have been successfully stored for long periods in sealed containers at low moisture levels under refrigeration (Zasada and Little, 2008). As expected, the measured temperatures at 5 and 10 cm soil depths were more uniform relative to air temperatures, as were the moisture conditions, and these likely account for the stable germination rates observed for the soil-incubated seeds. We observed a 50% drop in germination for forest litter-incubated seeds between 2011 and 2012, which was likely due to the large difference in annual precipitation, with 510 mm less rainfall recorded in 2012. We also tested germination rates for seeds stored under laboratory conditions for over the five plus years and observed only a small decrease (~3%) in germination rates relative to freshly collected cold-stratified seeds (87%). Wickert et al., (2017) reported germination rates of 0–27% for *Ailanthus* seeds stored under laboratory conditions for 8 years.

In addition to weather impacting seed viability, seed exposure to predators and diseases increases with time (Janzen, 1971; Chambers and MacMahon, 1994). Evidence of non-native earthworm activity was observed during later retrievals of seed bag which likely reduced leaf litter, and altered the microenvironment and soil structure (Hendrix and Bohlen, 2002). Little evidence of seed predation was observed during the first four retrievals ranging from 0 to 4% per seed plot replicate. In the 2016 retrieval, predation remained low (0–1.1%) in the soil-buried seeds, but higher for those incubated in oak leaf litter (> 25%), especially when litter cover was scant. Facelli (1994) reported that leaf litter may reduce seed predation. After five seasons, our recovery of seeds incubated in oak leaf litter was almost half the recovery rate of seeds incubated in soils (99%). Given that the 5-year-old buried seeds representing eleven sources averaged 79% germination, it is likely that many of them may have persisted, and remained viable well beyond the termination of this study. Typically the majority of seeds most often occur in the litter and upper 5 cm mineral soil layer in North American forests, but ample viable seeds have been recovered at 10 cm depths following disturbance (Moore and Wein, 1977, McGee and Feller, 1993, Stark et al., 2006). Since our previous work demonstrated that timber harvesting within 20 years was the primary predictor of *Ailanthus* presence and prescribed fire was not (Rebbeck et al., 2017), we were interested in determining if *Ailanthus* seeds could remain viable at soil depths resulting from forest floor disturbances created by heavy logging machinery. The level of germination after five years suggests that subsequent timber harvesting or prescribed fire operations might disturb soil and expose seeds to environmental conditions more conducive to germination and subsequent seedling establishment. Qi and Scarratt (1998) investigated the effects of harvesting method on seed bank dynamics and reported that severe disturbance created by logging equipment or site preparation may actually enhance the chances of successful germination of deeply buried seeds.

There was significant variability among the germination rates of the eleven seed sources studied at the start and end of the incubations. For those incubated in oak leaf litter, seeds from five of the sources did germinate after six years, albeit low (2–8%). Germination rates of soil-incubated seeds, ranged from 48 to 95% among the eleven seed sources after five years. Although variability among areas of collection was observed, more tree to tree variability was observed within a collection area. For example, the variability among the four seed sources within Delaware County ranged from 46 to 66%. Wickert et al. (2017) reported high variability in seed germination among seven trees of varying age and size ranged from 3 to 78%.

5. Conclusions and management recommendations

Our findings validate that *Ailanthus* seeds can remain viable for at least 6 years following natural- or human-caused disturbances which bury seeds, which is well beyond the previously described 2 year seed bank (Kota et al., 2007; Kowarik and Säumel, 2007). Having the knowledge that an individual female tree has the potential of producing a million seeds (Wickert et al., 2017) which maintain high viability (~79%) beyond five years, demonstrates the urgent need to proactively control this species. Based on our findings, we suggest extending the recommended time of removing female trees at a minimum of one year prior to a timber harvest (Kota et al., 2007) to more than six years to lower the rate of spread of *Ailanthus*. Given that buried *Ailanthus* seed can remain viable despite amble moisture and cyclic elevated temperatures, it is crucial to incorporate active mapping and control practices of *Ailanthus* as part of routine management operations to minimize its threat as an invasive species.

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