Seed longevity and dormancy state in an invasive tree species: *Ailanthus altissima* (Simaroubaceae)[1]

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Abstract. Successional tree species often form soil seedbanks, suggesting that extended seed dormancy may also facilitate regeneration in nonnative species. We examined seed dormancy in *Ailanthus altissima*, which is currently spreading into long-established forests of Europe and eastern North America. *Ailanthus* seeds were sewn into replicated nylon mesh bags and buried in 10 second-growth stands in southeast Ohio, USA. North- and south-facing slopes were included as a coarse-grained test for environmental control. Bags were recovered at 2-mo intervals and seeds were tested for viability and germination. Fifty percent of *Ailanthus* seeds survived the full length of the study (24 mo) after an initial phase of partial germination (51–79% of viable seeds). Remaining seeds returned to a state of induced dormancy, allowing a second flush of germination (3–28%) after 18 mo. After the first 5 mo no further decline in seed number was observed, suggesting persistence in the soil well beyond the 2-yr length of this study. No slope-aspect effect was observed. Long-term seed dormancy potentially facilitates *Ailanthus* invasion by buffering against extended canopy closure or allowing passive dispersal with movement of soil. Complete eradication of a population will depend on elimination of the soil seed bank, which may require many years. Management should avoid creating canopy openings near existing populations with the goal of suppressing sexual reproduction and seedling establishment.

Key words: disturbance, gap, invasion, seed bank, tree of heaven

Deciduous forests of eastern North America are relatively free of nonnative woody species. Many woody species have been introduced, and some are occasionally found in successional stands, but few persist as the forest matures (*e.g.*, Harrelson and Cantino 2006, Holmes and Matlack 2017), presumably excluded by competition from native species. Thus, height, broad seed dispersal, high fecundity, and vegetative longevity (traits that define trees) do not, alone, promote invasiveness. However, a few nonnative tree species have become invasive (*e.g.*, *Melalucca quinquenervia*, *Casurina equisetifolia*, and *Tamarix ramosissima* in North America), and North American *Pinus* species (particularly *P. radiata*) are problematic in other parts of the world. *Ailanthus altissima* is a notable example, a small tree from East Asia currently expanding populations in the Middle Atlantic and Central Hardwoods regions and in parts of Europe (Kasson, Davis, and Davis 2013).

Ailanthus altissima's success suggests that it possesses distinctive morphological, physiological, or life-history traits that enable invasion, and poses the larger question of how particular traits enable woody invasions in general. Invasiveness has been linked to *Ailanthus*' exceptional fecundity, growth rate, vegetative propagation, and dispersal range (Zasada and Little 2008, Knusel *et al*. 2017). Seed dormancy also potentially contributes to invasiveness, but little is known about this particular species. To test the potential of dormancy to promote invasion in *Ailanthus*, we documented seed longevity and seasonal dormancy condition in a natural forest community through 2 yr.

Seed dormancy can be viewed as an evolutionary response to seasonally unfavorable conditions for germination and establishment (Harper 1957). Seeds of herbaceous species often cycle through degrees of dormancy as appropriate to transient opportunities/risks for seedlings (Thompson and Grime 1979; Baskin and Baskin 1985; Honek, Martinkova, and Jarosik 1999). An embryo may switch into a germinable condition controlled by a simple environmental cue ("enforced dormancy"; Harper 1957) in a period suitable for seedling establishment (*e.g.*, Honek, Martinkova, and Jarosik 1999). Alternatively, the seed may remain

insensitive to the environment ("innate" or "induced" dormancy), allowing it to avoid unfavorable periods such as temperate-zone winter. Many species show polymorphic dormancy, in which a fraction of the seed crop is committed to each form of dormancy (Thompson and Grime 1979), which can be interpreted as a form of bet-hedging in an unpredictable environment (Rees 1993, Pake and Venable 1996).

Dormancy potentially facilitates invasion by stabilizing small colonist populations against stochastic variation in recruitment, mortality, and reproduction (Davis 2006). Invasive herb species typically show either transient (< 1 yr) or short-term persistent (< 4 yr) dormancy in the soil (Van Clef and Stiles 2001, Krinke et al. 2005, Liu and Pemberton 2008, DiTommaso et al. 2017), but even relatively brief dormancy may be sufficient to ensure invasive population persistence (e.g., Gibson, Spyeareas, and Benedict 2002; Webster et al. 2008).

Woody invasive species have occasionally been reported in forest seed banks (e.g., Paulownia tomentosa; Hyatt and Casper 2000) and seed banks of seminatural urban stands (A. altissima, Morus alba, and Celastrus orbiculatus; Kostel-Hughes, Young, and Carrreiro 1998). It is possible that these species have the capacity for multiyear persistence in the soil, although their presence may also indicate frequent seed input or exceptional conditions for persistence at isolated sites.

Ailanthus altissima (Mill.) Swingle (hereafter Ailanthus) is a small- to medium-stature deciduous tree native to eastern China. Ailanthus has a weedy life history (sensu Baker 1974, Richardson 1998) that contributes to its invasiveness (Fryer 2010). Seed production is prodigious; a single individual can produce more than 300,000 wind-dispersed seeds annually. Seeds mature in late fall and disperse throughout the fall, winter, and spring (Landenberger, Kota, and McGraw 2007; Wickert et al. 2017), typically germinating in the spring and early summer. Seedlings show best survivor-ship and growth in full sun—they appear to be intolerant of shade and wet soil (Martin and Canham 2010). Within sites Ailanthus propagates vegetatively, capable of extending clonal ramets as much as 15–30 m from the point of germination (Kowarik and Säumel 2007). Vegetative shoots of Ailanthus grow faster than seedlings and tolerate lower light levels, potentially facilitating coloniza-tion of shady sites (Knusel et al. 2017).

Although best known as a colonist of urban sites and abandoned agricultural land (Buell, Buell, and Small 1971), Ailanthus also has the capacity to invade mature forest, observed at sites in West Virginia, New York, Pennsylvania, and Ohio (Kowarik 1995, Knapp and Canham 2000, Reb-beck et al. 2017). Colonization depends on openings in the crown canopy (Grime 1965, Knapp and Canham 2000), and may be facilitated by natural disturbances such as tree-fall gaps, insect defoliation, and rock falls (Orwig and Foster 1998; Arnaboldi, Conedera, and Maspoli 2002; Espenschied-Reilly and Runkle 2008). Human disturbances such as timber harvest, invasive eradication programs, and prescribed burning can also initiate populations (Call and Nilsen 2003, Rebbeck et al. 2017). Areas along streams or rivers seem particularly vulnerable (Kowarik and Säumel 2007).

Dormancy. Freshly collected Ailanthus seeds commonly show 75–96% germination in the lab, implying 4–25% innate or induced dormancy (Zasada and Little 2008). Cold treatment improves germination (Graves 1990, Wickert et al. 2017), potentially allowing the species to avoid winter germination and increasing the chance of spring-time seedling emergence. Seeds may survive in the lab for 7–9 yr (Wickert et al. 2017) and 60% germination was observed after 2 yr of storage in a lab setting (Hildebrand 2006), but longevity in the soil is reported to be modest (< 1 yr; Krussman 1984; Kota, Landenberger, and McGraw 2007; but see Kaproth and McGraw 2008). Viable seeds have been reported from forest seed banks, but these are assumed to be transient (Landenberger, Kota, and McGraw 2007; Zasada and Little 2008). However, recent work (Rebbeck and Jolliff 2018) shows that Ailanthus can potentially survive up to 5 yr in natural settings, and suggests that the amount of germination depends on the seed microenvironment. Germination and establishment requirements are quite broad (Fryer 2010), appar-ently depending on light and elevation (Constan-Nava and Bonet 2012).

Little is known about dormancy states in Ailanthus or how dormancy fits into the larger demographic context of invasion. In this paper we examine seed longevity and seasonal dormancy condition in the soil to assess the potential of dormancy to facilitate invasion. Examination of a single species does not allow a general statement about woody species' invasions; our objective is

simply to document dormancy condition in this particularly problematic species and suggest implications for management.

Methods. Seed longevity and dormancy state were examined in 10 deciduous forest sites on the Allegheny Plateau of southeast Ohio (39°21′N, 82°24′W). Soils are well-drained, organic-rich sandy and silt loams typical of long-established forest in the region (Lucht *et al*. 1985). Natural vegetation is a mixed deciduous forest dominated by *Quercus, Carya,* and *Acer* species, with *Fagus grandifolia, Platanus occidentalis,* and *Liriodendron tulipifera* also appearing depending on landscape position and land use history (Braun 2001). The herb and shrub layers differ in composition between north- and south-facing slopes, reflecting microsite variation in moisture, litter depth, temperature, and day length (Olivero and Hix 1998; Goebel, Hix, and Semko-Duncan 2005). All study sites were situated on gentle to moderate slopes with a closed crown canopy and a moderate litter layer. Sites were selected to minimize fine-scale environmental heterogeneity (*e.g.*, microtopography, canopy gaps, tree proximity) allowing us to focus on variation in season and aspect. Sites were separated by at least 1 km to avoid autocorrelation of environmental variables and ensure statistical independence.

We examined seed longevity and dormancy condition by burying seeds in small nylon bags and recovering them at intervals following the method of Sarukhan (1974). Bag fabric had a 0.1-mm mesh, allowing water and gas exchange but excluding seed predators. Seeds were collected in two wild populations near our lab in Athens, OH in December, 2010 and thoroughly mixed to remove potential variability between source populations and parent genotypes. Air-dry seeds were stored in the laboratory at ambient temperature (18–20 °C) for 1–2 wk before sewing them into bags and transferring to the field sites. Only apparently healthy seeds were used, i.e. firm seeds, rounded in shape, and showing no evidence of predation, fungal infection, or desiccation. One hundred seeds were counted into each bag, and bags were deployed in mid-December, approximating the season of natural seed dispersal (Fryer 2010). Bags were placed on the mineral soil surface under the litter and duff layers to mimic natural seed deposition.

Dormancy condition potentially responds to environmental cues (*e.g.*, Honek, Martinkova, and Jarosik 1999; Wainwright and Cleland 2013), and the environmental factors that define herb and shrub communities in this ecosystem also may be expected to influence dormancy condition. Thus, to provide a coarse-grained test for environmental control of dormancy, burial sites were selected on both north- and south-facing slopes using slope as a proxy for a suite of underlying environmental variables. Bags were recovered at 2-mo intervals for 24 mo. The complete design included 5 replicate sites by 2 slope aspects by 12 recovery dates = 120 bags, with 100 seeds in each bag.

Recovered seeds were tested for germination on moist filter paper in the laboratory. Lab germination implies a state of enforced dormancy (Harper 1957) in which activation of the embryo awaits some form of environmental cue. Lack of germination of viable seeds implies innate or induced dormancy in which germination is suppressed by immaturity of the embryo or presence of a physical or chemical inhibitor. Germination was defined as cracking of the seed coat followed by emergence of a radicle. Seeds were tested at ambient temperature (18–20 °C) under fluorescent lighting (*ca*. 12/12-hr photocycle) for 2 wk, after which germination had ceased in all samples. Seeds that did not germinate were tested for viability by visually observing the embryo for firmness and a yellow or green color. Tetrazolium tests (Huebner 2011) were not used because seeds had already imbibed water from germination testing and did not readily absorb the tetrazolium solution. The visual and tetrazolium methods agreed strongly (99–100%) in trials using unimbibed seeds, so visual examination was considered acceptable.

Change in dormancy status was measured as the difference in seed viability and germination fraction between samples recovered at successive dates.

Change in viability =
$$(\text{Seeds germinating} + \text{dormant})_{t+1}$$
$$- (\text{Seeds germinating} + \text{dormant})_{t}$$

Change in germination fraction =
$$\frac{\text{Seeds germinating}_{t+1}}{\text{Seeds alive}_{t+1}} - \frac{\text{Seeds germinating}_{t}}{\text{Seeds alive}_{t}}$$

The total number of surviving seeds (those that germinated in the lab plus those alive but not germinating) plotted across recovery dates can be interpreted as a survivorship curve. However,
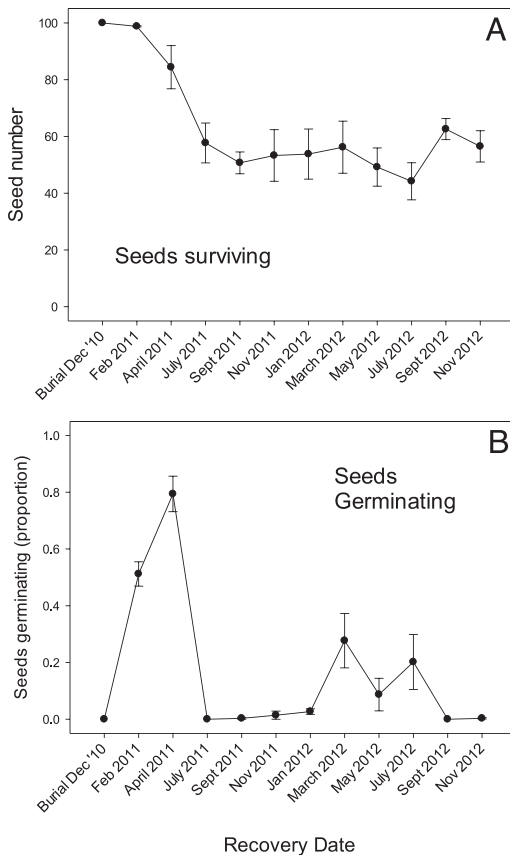
FIG. 1. Longevity and dormancy condition of *Ailanthus altissima* seeds buried in long-established forest sites. (A) Live seeds surviving at 2-mo intervals. (B) Proportion of live seeds germinating in laboratory trials. Means and standard errors.

because sampling was destructive and each sampling date represents a separate group of seeds, we do not know the fate of individual seeds. Uncertainty about dates of mortality leads to intractable problems of right-censoring (Crawley 2007), so conventional survival analysis could not be used. Instead, we compared the total number of surviving seeds using a generalized linear model (GLM) set up as an analysis of covariance (Package GLM) in which sites were treated as replicates and a Poisson error distribution was assumed. Slope aspect was entered as a categorical variable and recovery date (number of months in the soil) as a covariate. A similar analysis was applied to germination fraction, described as the proportion of all surviving seeds that germinated at each recovery date; an arcsin square-root transformation was applied as appropriate to proportional

data. All procedures were conducted in the R statistical environment (R Core Team 2013).

Results. *Ailanthus* seeds declined in viability by ~40% through the first spring and summer (February–September 2011), but numbers of surviving seeds were stable thereafter (Fig. 1a). Close to 50% remained viable at the end of the experiment. Log-transformed seed numbers were significantly related to recovery date (GLM; coefficient = −0.025, $|t| = 3.373$, $P = 0.0005$) but not to aspect ($P > 0.05$). Germination was strong (51–79%) in the first year (Fig. 1b) and distinctly seasonal, concentrated in late winter and spring, which corresponds to the natural germination period. In the second year, the timing was similar, but a lower proportion (3–28%) germinated. Germination showed a significant date effect (coefficient = −0.032, $|t| = 2.317$, $P = 0.0225$). *Ailanthus* experienced 23.6% higher germination in seeds recovered from north-facing slopes than south-facing in April 2011 and 11% higher germination on north-facing slopes than south-facing in September 2011, although the difference was not significant across sample dates ($P > 0.05$).

Discussion. Extended dormancy of *Ailanthus* described here provides a marked contrast with most native woody species in deciduous forests of eastern North America (Baskin and Baskin 2000), and with most previous reports for *Ailanthus* (Landenberger, Kota, and McGraw 2007; Zasada and Little 2008), but dormancy is consistent with behavior of some successional and invasive species (Hille Ris Lambers, Clark, and Lavine 2005) and with a recent report of *Ailanthus* (Rebbeck and Jolliff 2018). Our results allow changes in dormancy state to be interpreted with bimonthly resolution, shedding new light on the demographic and adaptive function of extended dormancy.

A brief period of winter dormancy ensured *Ailanthus* seeds were available for germination in the first spring. The large germinable fraction (up to 80% enforced dormancy) observed in February–April 2011 is consistent with previous reports of brief dormancy, nonspecific germination requirements (Hunter 2000, Evans *et al.* 2006, Fryer 2010), and a germinating fraction as high as 64–98% (Bory and Clair-Maczulajtys 1977, Singh, Gupta, and Chand 1992). Early and massive germination can be understood in terms of limited opportunities for establishment, which are defined

in *Ailanthus* by closure of the forest canopy in springtime and the shade intolerance of seedlings (Forgione 1993; Espenschied-Reilly and Runkle 2008). On a longer timescale, the rapid decline in light quality as canopy gaps close places a premium on sensitivity to the light environment and rapid germination when light becomes available (Kota, Landenberger, and McGraw 2007). Indeed, seedling establishment rarely occurs beyond the first and second year after gap formation (Knapp and Canham 2000).

Seeds surviving the initial period of germination (*ca.* 50% survival) entered a condition of induced dormancy that continued for 2 yr until the end of the experiment. Extended dormancy allowed *Ailanthus* to produce a second flush of germination in year 2, and germination would presumably occur in later years if given the opportunity. Consistent with our observation, a small portion of experimentally sown *Ailanthus* survived to germinate in the second year at field sites in West Virginia (Kota, Landenberger, and McGraw 2007; and see Hildebrand 2006). Longevity up to 5 yr has been reported at a field site in Ohio (Rebbeck and Jolliff 2018). Undoubtedly, slightly different results would be obtained if we had used different test conditions, but the important observation, a large nongerminating fraction distributing germination over 2 yr, seems robust and consistent with previous studies.

After the initial flush of germination, *Ailanthus* would be considered to have a type IV persistent seed bank (Thompson and Grime 1979), with large dormant reserves surviving from year to year and a relatively small fraction becoming seasonally germinable in each year. This behavior is more similar to invasive *Acacia* species in fire-shaped South African ecosystems (Richardson and Kluge 2008) than to native North American species most of which show little dormancy. Our findings contradict statements in several management-oriented reviews; *Ailanthus* is generally assumed to have no long-term seed dormancy (Krussman 1984) and, thus, not to form soil seed banks (Hunter 2000, Evans *et al.* 2006). However, these assertions have not been based on rigorous testing in a natural forest community.

Invasion of Temperate-Deciduous Forest. Polymorphic dormancy states can be interpreted as a form of bet-hedging in which the proportion of germinable seeds reflects the predictability of conditions favorable for seedling establishment (Rees 1993, Pake and Venable 1996). The relatively large fraction of buried seeds that remained dormant (30–50% in year 1) potentially represents an adaptation to uncertain seasonal and annual opportunities for germination (Densmore 1979; Richardson and Kluge 2008). The evolutionary context of *Ailanthus* dormancy is unknown, but rapid invasion in eastern North America implies that its life history, including seed dormancy, is well-suited to the disturbance dynamic of deciduous forest.

Ailanthus enters forest stands by colonizing tree-fall gaps and human-generated disturbances. Seeds presumably arrive by wind or as hitchhikers on vehicles and equipment. As foliage grows into the gap and the canopy closes, a strategy of ramet banking allows *Ailanthus* to survive shade and respond rapidly when light becomes available again (Kowarik and Säumel 2007, Rebbeck *et al.* 2017). Thus, clonal propagation in *Ailanthus* serves the function of seed banks in many weedy and successional species (Harper 1977). In contrast to its vigorous clonal propagation, *Ailanthus* seedling establishment is rare in North American forests despite a heavy seed rain (Martin and Canham 2010). Infrequent seedling establishment suggests that the seed banking observed here has little effect on population growth in American forests, although it presumably plays a role in the species' native ecosystem.

The ecological ramifications of our dormancy results are unclear. We assume that in some unspecified situation, dormant seeds allow survival of conditions unsuitable for vegetative growth. For example, dormancy may allow invasion of undisturbed sites by delaying germination until disturbance occurs. Alternatively dormant seeds may remain viable in the soil longer than shaded ramets can survive after canopy closure, thereby increasing the chances of persistence until disturbance reopens the canopy. A similar strategy is used by the invasive tree *Pawlonia tomentosa*, a prolific, wind-dispersed species in which seed dormancy allows opportunistic use of local disturbances (Hyatt and Casper 2000, Innes 2009). Some native species appear to use seed banking to survive unsuitable periods during old-field succession (Marks 1974; Sutherland, Hutchnison, and Windus 2003; Hille Ris Lambers, Clark, and Lavine 2005). The similarity of dormancy behavior to these native species suggests that *Ailanthus* has been

successful as an invader because its dormancy behavior fits a pre-existing niche.

It is also possible that seed dormancy benefits *Ailanthus* by promoting spatial dispersal. Dormancy may facilitate invasion by allowing passive dispersal by processes that move soil, such as transport by rain wash or human movement of soil or gravel (Richardson *et al.* 2007, Miller and Matlack 2010) in addition to its temporal buffering function.

Management Recommendations. If *Ailanthus* can persist in closed-canopy sites as dormant seeds, as work here suggests, and germinates when disturbance opens the crown canopy, then eradication efforts aimed at the vegetative phase will be frustrated. Further research is needed to determine the extent to which *Ailanthus* actually forms long-term soil seed banks in invaded sites, and under what circumstances those seeds will germinate.

In the meantime, the best defense against invasion appears to be an intact forest canopy that suppresses sexual reproduction and seedling establishment. Management efforts should avoid creation of gaps near existing *Ailanthus* populations. A strategy directed to preventing colonization of new sites, which have neither seed nor ramet banks, is probably more effective than trying to remove established populations from already-colonized sites (Richardson and Kluge 2008).

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