The Effect of Silviculture Management on the Spread of Three Invasive Species

A thesis presented to

the faculty of

the College of Arts and Sciences of Ohio University

In partial fulfillment

of the requirements for the degree

Master of Science

Mame S. Redwood

June 2012

This thesis titled

The Effect of Silviculture Management on the Spread of Three Invasive Species

by

MAME S. REDWOOD

has been approved for

the Department of Environmental and Plant Biology

and the College of Arts and Sciences by

Glenn R. Matlack

Associate Professor of Environmental and Plant Biology

Howard Dewald

Interim Dean, College of Arts and Sciences

ABSTRACT

REDWOOD, MAME S., M.S., June 2012, Environmental and Plant Biology

The Effect of Silviculture Management on the Spread of Three Invasive Species

Director of Thesis: Glenn R. Matlack

Disturbance such as forest management is thought to promote invasive species spread. This study uses population demography to address the spread of the invasive species *Ailanthus altissima, Alliaria petiolata,* and *Microstegium vimineum* in forested sites in southeast Ohio.

Invasive species populations were examined in the silvicultural treatments prescribed burn and timber harvest, plus control plots with no management. Seed rain, seedling establishment, and the soil seed bank was studied for each population.

All invasive seeds formed a persistent seed bank and experienced seasonal dormancy, but the proportion of dormant seeds varied among species ($p<0.05$). Slope aspect effected seed survivorship and dormancy ($p<0.05$) for each species. Dormancy for each species showed no relationship or a weak relationship with time since seed burial.

Invasive populations expanded at a constant rate among treatments, and invasive seeds changed dormancy conditions seasonally to allow for germination during favorable conditions, which may contribute to invasive ability.

Approved: ____

Glenn R. Matlack

Associate Professor of Environmental and Plant Biology

ACKNOWLEDGMENTS

Thanks to Dr. Cynthia Huebner and the Northern Research Station, US Forest Service for funding and Ohio Department of Natural Resources for permission to study in state forests. Thanks to committee members Dr. Stefan Gleissberg and Dr. Harvey Ballard, labfellows Erik Niederhauser and Jennifer Philhower-Gillen, and Keith Gilland for advice with statistics.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

This study examines the possibility that timber harvest and prescribed burning facilitate invasive species spread. Increased light availability and soil disturbance from a harvest and soil exposure caused by prescribed burning have both been shown to have a positive effect on invasive species population growth in deciduous forest (Meekins and McCarthy 2001, Glasgow and Matlack 2007, Gorchov et al. 2011), suggesting a connection between forest management and invasion. The question of invasion facilitation is critical to the future of oak forests because invasive populations are potentially competing with tree seedlings, impeding forest regeneration after harvest (Oswalt et al. 2007).

The spread of a plant population can be modeled as a simple diffusion process:

$$C = 2\sqrt{D\lambda}$$

(Okubo and Levin 2001). The dispersal coefficient (D), which expresses area colonized per unit of time, and reproductive rate (λ) determine the rate of diffusive spread I. In this model, each seed travels a random distance within the modeled dispersal range in any direction. At a coarse scale the collective effect of seed movements over many generations is a wave front moving at a predictable rate (Andow 1990). Fine scale variation in D and λ is reflected in the coarse scale diffusion rate. In the present study, invasive species demography is compared between three management regimes to test for an effect of management on D and λ, and thereby to predict the effect of management on population expansion.

Forest disturbance and invasion dynamics

The forest canopy determines the character of the deciduous forest understory, so heterogeneity in the canopy may be expected to affect the establishment and expansion of invasive species in the understory. Closed-canopy forest is invaded less often than those with a disturbed canopy (Rouget and Richardson 2003, Matlack and Schaub 2011). Natural canopy gaps and anthropogenic timber harvest are two forms of disturbance that increase light availability in the understory and both have been shown to affect understory community dynamics. For example, the invasive species *Rubus phoenicolasius* requires a canopy gap to establish, but persists after the gap has closed (Gorchov et al. 2011). *Microstegium vimineum* and *Rosa multiflora* have been shown to have higher germination in canopy gaps (Glasgow and Matlack 2007). Invasive species have also been shown to have higher germination on bare soil (Meekins and McCarthy 2001, Bartuszevige et al. 2007, Glasgow and Matlack 2007, de Villalobos et al. 2010) as might be created by timber harvest or prescribed burning. The effect of canopy and soil disturbance on invasive species spread is a deviation from the diffusive expansion model described above because spatial variation in the environment affects the probability of seedling establishment, an element of D, and resource availability affects population growth rate. Timber harvest and prescribed burning open the canopy and expose the soil, so it is possible that these actions help to expand invasive species populations (Veldman et al. 2009).

Seed dormancy and population expansion

Invasive species often persist as dormant seeds in the soil which potentially allows them to respond to canopy and soil disturbance. The dynamics of seed banks are not well understood in invasive species but we can infer their behavior by examination of native species. Seed dormancy allows a species to persist until a disturbance increases resource availability and allows for vigorous growth and high fecundity (Thompson and Grime 1979, Oswalt et al. 2007). Furthermore, dormancy allows seeds to germinate at a favorable time in an environment that fluctuates seasonally (Sarukhán 1974, Thompson and Grime 1979). Both transient and persistent seed banks have been observed in invasive species (Martinez-Ghersa et. al 2000). The invasive grass *M. vimineum* persists for three years (Barden 1987) and *A. petiolata* has been shown to have a seed bank that persists for ten years (Nuzzo 2000). Early-successional species are the primary component of forest seed banks, even after the canopy has closed and no such species are present in the above-ground community, implying that the seed bank is mainly formed early in succession (Pickett and McDonnell 1989, Hyatt and Casper 2000). Seeds that do not die underground remain in the seed bank until a canopy gap re-creates early-successional conditions which allow recruitment of both native and invasive light-demanding species (Thomson and Grime 1979, Oswalt et. al 2007).

Woody perennials often survive without a seed bank, surviving periods unsuitable for recruitment as suppressed seedlings on the forest floor. These seedlings can be thought of as analogous to a seed bank because the seedlings are eventually recruited into the canopy, much as seeds are recruited to the population (Canham 1985). However, these seedlings are more susceptible to death during a disturbance than buried seeds (seeds, however, are susceptible to death by predators, fungus, and unsuccessful germination). An invasive tree would be expected to have a seedling bank, but a species with the ability to form a seed bank would be more disturbance-tolerant than its seedling-dependent neighbors.

The type of dormancy experienced by the seed is important to invasion because dormancy type determines whether the species will form a persistent or transient seed bank, and whether the seed bank will become germinable after a disturbance. Harper (1957) classified dormancy based upon embryo maturity and germination requirement. “Innate” dormancy is caused by qualities of the seed such as an immature embryo or strict germination requirements (such as photoperiod). This type of dormancy allows a seed to germinate only after passage of time, making it independent of short-term environmental variation. “Enforced” dormancy is imposed by unfavorable environmental conditions, and dormancy is lifted when the environment becomes favorable. “Induced” dormancy occurs when a seed that experienced enforced dormancy does not germinate after environmental conditions become favorable because new germination requirements have developed. The new germination requirement is often exposure to light, which occurs after soil disturbance. Dormancy is responsible for the long-term accumulation of seeds in the soil seed bank (Sarukhán 1974). The present study examines the types of dormancy experienced by three invasive species and explains the consequences of dormancy type changes through time.

A plant's capacity for dormancy tells us whether a population can survive a disturbance that prevents seed set for one or more years (such as herbicide application). This attribute is especially important for the control of invasive plants. The comparison of invasive species to native species can be used to determine whether invasives have particular life history attributes that may enhance invasive ability.

Invasive species and forest regeneration

The long-term persistence of a forest depends upon regeneration of canopy trees by seedlings, and invasive species threaten forests by competing with tree seedlings. Reduced growth and survival of native woody tree seedlings have been inflicted by the invasive species *Microstegium vimineum, Alliaria petiolata,* and *Ailanthus altissima* (Meekins and McCarthy 1999; Call and Nilson 2005; Marshall et al. 2009, Flory and Clay 2010). A negative linear relationship between percent cover of non-native invasive species and stem density of native woody seedlings and saplings was found following tree canopy harvest in Tennesee (Oswalt et al. 2007) suggesting that cover of non-native species inhibits survival or establishment of native saplings. Presence of invasive species has also been shown to reduce species diversity in deciduous forests (Oswalt et al. 2007) and removal of invasive species from lowland wet forest has been shown to increase native species richness (Baider and Florens 2011). This empirical evidence suggests that invasions are potentially a threat to forest regeneration.

Forest management techniques are a form of human-mediated disturbance with the potential to promote invasion. In a late-successional forest, a canopy opening is the product of a natural or anthropogenic disturbance event. Anthropogenic creation of roads, firelines, and timber harvest all require tree removal and movement of heavy equipment, resulting in canopy gaps and disturbed soil which are susceptible to invasion. For example, roads and human developments in Rocky Mountain National Park have the highest abundance of the invasive species *Bromus tectorum* (Banks and Baker 2011), and harvested forests in Tennessee experienced rapid and dramatic population expansion of the invasive grass *Microstegium vimineum* post-disturbance (Oswalt et al. 2007). Selective timber harvest and prescribed burning are two management techniques thought to promote oak regeneration in Appalachian forests (Abrams, 1992, 1998, 2003; Lorimer et al., 1994; Sutherland et al., 2003) but they also potentially promote invasion.

It is known that invasive species thrive in disturbed habitats such as managed forests, but it is unknown how the demographic characteristics of invasive populations differ between disturbed and undisturbed forest. The problematic effects of *Microstegium vimineum, Ailanthus altissima,* and *Alliaria petiolata* on deciduous forest make it important to discover how these species respond to management. This study examines seed rain, seedling establishment, seed dormancy, and germination to measure population expansion. These measures are used to determine spatial dispersal and population growth rate, variables in the diffusive invasion model, to ask the questions: How does demography influence population expansion, and how can that insight be used to understand the response of invasive species to forest management?

MATERIALS AND METHODS

Study Species

The three study species are common invasive plants in southeast Ohio. They have different growth forms and life histories, yet they all have been known to invade intact deciduous forest ecosystems and are considered major challenges to land managers in the region. *Microstegium vimineum* (Poaceae) is an annual C_4 grass from southeast Asia, which was first found in the United States near Knoxville, Tennessee in 1919 and is now common throughout the eastern United States, including the Ohio Hills region of the Allegheny Plateau (Fairbrothers and Gray 1972, Huebner 2011). *Microstegium vimineum* occurs in hydric-mesic forest, often on stream terraces, floodplains, and along anthropogenic dispersal corridors such as roads and trails (Gibson et al. 2002, Miller and Matlack 2010). Colonization and population expansion are associated with canopy openness and soil disturbance (Glasgow and Matlack 2007, Oswalt et al. 2007). *M. vimineum* emerges in late May or early June, sets seed in late September, and has small seeds without an obvious dispersal mechanism (Gibson 2002). *M. vimineum* is shade-tolerant and can exist at light levels as low as 1% full sunlight by utilizing sunflecks (Horton and Neufield 1998) but fecundity and biomass decline below 18% full sunlight (Claridge and Franklin 2002, Huebner 2011). Suppressed individuals may have just one stem per plant, but in areas of sufficient light and moisture, many stems may occur on one horizontal stem of an individual (Huebner 2011). Individuals may reach 1.5 m in height with one or two terminal inflorescences of chasmogamous flowers per stem

(Huebner 2011). Cleistogamous flowers occur in a culm along the basal stem (Tu 2000). The seeds of *M. vimineum* are believed to have a maximum dormancy period of three years in the soil (Gibson 2002).

Alliaria petiolata (Brassicaceae) is a biennial herb from Europe which was first documented in the United States in New York in 1868 (Meekins and McCarthy 1999). *Alliaria petiolata* is found in deciduous forests and roadsides throughout the Allegheny Plateau. *Alliaria petiolata* is most prolific in mesic deciduous forests with partial sun, but populations can persist in a wide range of habitats including xeric microsites such as ridgetops and railroad tracks (Nuzzo 2000). *Alliaria petiolata* germinates in early spring and produces a basal rosette that overwinters as a green plant. *Alliaria petiolata* bolts and flowers in early spring of its second year, sets seed in late spring, and is dead by mid-summer. The fruits are siliques containing 10-20 seeds each, with an average of 4-16 siliques per plant (Nuzzo 2000). *Alliaria petiolata* seeds experience a dormancy period of 6-18 months before germinating in the field (Cavers et al. 1979, Baskin and Baskin 1992) and have the ability to lay dormant in the soil for at least ten years (Nuzzo 2000). *A. petiolata* has small seeds without an obvious dispersal mechanism (McCarthy 1999), but the species is believed to be dispersed by humans based upon a positive relationship between human developments and *A. petiolata* distributions (Gavier-Pizarro et al. 2010).

Ailanthus altissima (Miller) Swingle is a small-stature deciduous, dioecious tree that was introduced in the United States in the late eighteenth century as an ornamental (Hu 1979). *Ailanthus altissima* is found in deciduous forest edges and urban areas throughout the Allegheny Plateau. *A. altissima* is known to thrive in poor soil and tolerate air pollution (Hu 1979) but is dependent upon gaps for colonization and is intolerant of shade and flooding (Knapp and Canham 2000). An individual *A. altissima* can produce more than 300,000 light, spiral samaras that mature in late fall and are released throughout the fall, winter, and spring (Landenberger 2007). Little is known about the ability of this species to form a seed bank. Individuals exhibit vigorous vegetative propagation via root sprouts, especially after being cut, which complicates attempts at mechanical control (Kostel-Hughes et al. 2005). *A. altissima* contains allelopathic compounds known to kill competing vegetation (Hu 1979, Gómez-Aparicio and Canham 2008).

Study sites

The sites studied were located in the Ohio Hills region of the Allegheny Plateau in oak and hickory-dominated forests and the Mid-Atlantic Ridge and Valley physiographic province of central West Virginia in oak-pine forests (Braun 2001). The sites were located in national and state forests, state parks, and on private land (See Appendix A for sites and coordinates). The soils of both regions are fine-textured weathered Ultisols but the Allegheny Plateau soil developed from a sandstone parent material and the Ridge and Valley soils are stony and originated from sandstone and conglomerate rock (Braun 2001). The Allegheny Plateau receives 102-145 cm of annual precipitation. The Ridge and Valley region in central West Virginia receives 80-90 cm of precipitation. The Ridge and Valley region has a higher elevation (1000-2000 feet) than the Allegheny Plateau and has a shorter frost-free growing season. Ridge and Valley forests are characterized by oak and pine species in the overstory, and the understory is dominated by ericaceous shrubs (Braun 2001). Within these regions, study sites were chosen in areas recently (within the last 5 years) subjected to one of four different management practices: (1) prescribed burn, (2) first-stage shelterwood harvest, (3) diameter-limit harvest, and (4) control sites with no recent fires or harvest.

"Shelterwood" harvest is a two-stage harvest technique intended to promote oak regeneration by removing subcanopy trees (50-75% of the total basal area) in the first stage harvest to increase light availability to oak seedlings but leave mature trees as seed trees and to buffer the full sun until seedlings grow sun leaves. Canopy trees are left for 5-10 years before being harvested (Nyland 2002). Clear-cutting and selective cutting are the most common methods performed by the Forest Service, but it has been proposed to increase shelterwood harvest to favor oak regeneration (Manongahela National Forest Plan 2006, Wayne National Forest Management Plant 2006). Increased light availability has been shown to decrease soil moisture along a gradient of shelterwood harvest intensity (Prevosto et al. 2011b). The shelterwoods studied had low residual basal area (25-40%), with large areas of 100% canopy openness broken up by intermittent patches of canopy trees. The shelterwood study plots were found on skid trails, which were areas of 100% canopy openness. However, dense early-successional growth of shrubs and vines such as *Rubus* and *Smilax* species occurred above the invasive species populations. The plots also had a high density of coarse woody debris.

"Diameter-limit cutting" (DLC) is a method often used by private landowners. In a DLC, trees above a certain diameter (often 16"-18") are harvested, which creates large gaps in the canopy that increase light availability, but the amount of residual basal area can vary greatly depending upon stand age (Nyland 2002, Nyland 2005). Residual basal area of the DLC studied was very high (<25% canopy removal), so the canopy gaps were discontinuous. Coarse woody debris existed on the forest floor in lower density than the shelterwood. Understory species and growth was typical of deciduous forest, except for the skid trails, which were densely populated with *M. vimineum*.

"Prescribed burning" is used to clear shrubs from the understory and is thought to promote oak regeneration by reducing competition with oak seedlings (Brose 2010). Burns at the study sites appeared to be low-intensity burns due to tree burn marks just a few inches off the ground and the presence of incompletely burned coarse woody debris (Keyser et al. 2008). The burned sites were characterized by linear corridors of land cleared of vegetation, enclosing a few acres at a time intended to act as a border and check the spread of the fire, known as "firelines".

Populations were chosen on N-NE-E aspects to reduce aspect-dependent variation (Small and McCarthy 2003). The control and burned sites that were found near road were <20 m from the forest edge, well within the 40 m edge zone (Matlack 1994). Control and burn site populations found beyond the edge zone in mature closed-canopy forest were always close to trails or firelines. Shelterwood and diameter-limit sites had more-open canopies and populations were often found on skid trails. In most populations, one or more edges extended all the way to a road, so if a transect intersected the road it was not sampled. Therefore, only two or three transects were studied in some populations. Population sizes ranged from 1 m^2 to 50 m^2. *Alliaria petiolata* sites were relatively low in density with 4-10 adults/m^2 in 2010. *Microstegium vimineum* sites were much denser with 200-250 stems/m^2. Density and population size measures indicate that *A. petiolata* populations had between 8 and 500 individuals while *M. vimineum* populations had between 28 and 12,500 stems. Populations with clearly defined edges were ideal but populations with diffuse edges were included to fill out the experimental design. The design remained incomplete due to difficulty in locating sites with proper treatment, species, and slope qualities. Furthermore, time for site scouting was limited because populations had to be found between the time of seedling emergence and seed set in 2010.

Table 1

M. vimineum experimental design

Species	Region	Control	Burn	SW Harvest	DLC
M. vimineum	Allegheny Plateau	2	3	2	1
M. vimineum	Ridge & Valley	2	0	2	0

Thus, *M. vimineum* was represented in diameter-limit cutting and replicated in controls, burns, and shelterwood harvest. Only one *A. altissima* site, a Diameter-limit cut site, met the criteria for inclusion. This site can provide positive seed dispersal results but the lack of replication makes negative results inconsequential. *A. petiolata* was represented by two control sites and two burn sites. No suitable *A. petiolata* sites were found in the Ridge and Valley province.

Field procedures

Population expansion was described by recording distance from the edge of each target population. The population edge was defined as a plot containing zero individuals of the target species adjacent to a plot containing at least one individual of the target species. Edge plots of *A. petiolata* had 4-10 individuals per m^2 and *M. vimineum* plots had on average 200-250 stems per m^2. Twenty-meter transects of twenty 1 x 1 m contiguous plots extended from the edge of the study population of *A. petiolata* and *M. vimineum* in the four cardinal directions. Transects extended 100 m from the *A. altissima* population, because the seeds of *A. altissima* are adapted for wind dispersal and have been documented dispersing up to 100 m from a source plant (Landenberger et al. 2007). To document the dispersal and successful establishment of each population and estimate each species' spread rate, stem density was recorded in a 1 m^2 plot within the population adjacent to the population edge, and in each plot on the 20 m^2 transect in 2010 and 2011. The horizontal stem connecting *M. vimineum* vertical stems was often covered by litter or tangled with other individuals, making it difficult to distinguish genetic individuals. To prevent disturbing *M. vimineum* populations, stem number rather than individuals was recorded. This design assesses the effect of time, direction, and distance on seedling establishment at the edge.

To document seed dispersal, seed traps were placed along the established transects. The placement of seed traps extended from the source population on a modified logarithmic scale to intensively sample the expected seed dispersal range and distribution (< 4 m) but to include greater distances since the dispersal range was unknown. Traps were placed at 0 m, 1 m, 2 m, 3 m, 4 m, 6 m, 9 m, 16 m, and 20 m along the 20 m transects during the first year of the study. Traps were placed every 5 m along the 100 m *A. altissima* transect. The distance from the population edge represented a radius of circular area sampled, so area sampled increased exponentially with distance from the population edge. To ensure a similar proportion of the area was sampled at each distance, seed trap size increased with distance from the population edge. In the first year of sampling, seeds were exclusively found in seed traps adjacent to the population edge (at 0 m on the 20 m transect), so the design was modified in the second year to sample distances at a finer scale. One 400 cm^2 (10 cm x 40 cm) *M. vimineum* trap was placed at each distance 1-10 cm, 30-40 cm, 60-70 cm, 90-100 cm, 2 m, 3m, and 4 m from the population edge. *A. petiolata* populations were not sampled in the second year because study populations exclusively consisted of first-year rosettes, which do not flower.

The seed traps for *A. petiolata* and *M. vimineum* were cardboard squares coated with Tanglefoot™ adhesive (The Tanglefoot Company, Grand Rapids, MI). A spatula was used to spread the adhesive on each square and a metal wire was pushed through the trap and into the soil to secure the trap to the ground. The seed traps for *A. altissima* were nylon mesh baskets 314 cm^2 (20 cm in diameter), which were designed for *A. altissima's* large, wind dispersed seeds following Landenberger et al. (2007). Traps were checked for seeds and cleaned of debris weekly, and replaced as needed during the fruiting season in 2010 and 2011. In addition to seed dispersal (potential spread), seedling establishment (effective spread) was quantified in the same plots and transects used for seed dispersal. To study seedling establishment, the distance from the population edge to each stem colonizing outside the population and to each stem <30 cm within the population edge was recorded in the second year of the study.

Few seeds appeared in seed traps, making the seed number too low to provide proper power for a statistical test, so dispersal was evaluated using seedling establishment data. I worked with the null hypothesis of diffusive spread, assuming random dispersal in random directions, and equal rate of spread in all treatments (Cain et al. 1998). Dispersal was evaluated by expressing the number of seedlings established 30 cm within the population edge and fitting negative exponential curves to the distribution of seeds with distance. This analysis implies the potential maximum distance of spread, and allows comparison of dispersal between treatments.

Significant differences in dispersal between treatments for each species were evaluated using a two-way Analysis of Covariance (ANCOVA) in R 2.12.1. Distance was treated as a continuous, dependent variable, frequency (expressed as stems/0.1m^2) was treated as a dependent variable and treatment was tested as a major factor. A parallel ANCOVA tested for a treatment x frequency interaction. To maximize variation within-site and therefore make the test more conservative, the four directional transects per site were lumped for analysis.

Seed bank procedures

To determine whether invasion is promoted by dormant seeds in the soil within and around the populations, soil samples were taken along each transect shortly after the time of natural seedling emergence in each treatment. Samples were taken after seedling emergence so the samples represented the minimum amount of dormant seed present during the year. Samples were taken at each of the 1 m^2 plots sampled with seed traps. Soil seed banks are known to be spatially heterogeneous, so five 5 x 5 x 5 cm^3 soil samples were taken at each 1 m^2 plot and pooled for testing. Samples were sieved through 2 mm mesh and samples from *A. altissima* plots were examined for root segments. The sieved soil from all treatments was spread on sand of 1 cm depth in trays and all trays were placed in a greenhouse with daytime temperatures between 30 and 35° C. The greenhouse was lit by high-pressure 1800-watt sodium lights for 14 continuous hours a day. To test that the greenhouse environment was conducive to invasive germinability, two control trays of forest soil with added stratified invasive seeds were included for each invasive species. Samples were kept moist and monitored for seedling emergence for eight weeks. Germinants of non-target species were removed, and target species were recorded and removed. Analysis of these data was not possible due to zero seedling emergence in most replicates. Three stems emerged in one 0 m (adjacent to the population edge) *M. vimineum* replicate, indicating a seed bank is present within but not beyond the established population. Zero stems emerged in *A. petiolata* replicates, but no seeds germinated in the control flat, indicating that greenhouse conditions may have suppressed germination.

Seed dormancy experimental design

Variation in dormancy type throughout the year and seed mortality rate was determined by burying mesh bags containing seeds of the three exotic study species and three native species. Each invasive was paired with a native species based on similar life histories. *A. altissima* was paired with *Acer saccharum* because *A. saccharum* is also a woody perennial with wind-dispersed seeds that is known to colonize gaps. *M. vimineum* was paired with *Lysimachia quadrifolia* because *M. vimineum* and *L. quadrifolia* have similar ranges and wetland indicator status (USDA plants database). *A. petiolata* was paired with *Eupatorium rugosum* because *A. petiolata* and *E. rugosum* have a similar range and a weedy life history (USDA plants database).

One hundred seeds of an invasive species and 100 seeds of its paired native species were placed in each bag for a total of 200 seeds per bag. *M. vimineum, A. altissima, A. petiolata,* and *A. saccharum* seeds were collected from the wild while *L. quadrifolia* and *E. rugosum* seeds were bought from a commercial retailer. The bags were deployed shortly after the time of natural seed dispersal in summer and late fall. Seed bags were placed at the soil surface to mimic seed dispersal. *A. petiolata* seed bags were deployed in late July 2010, *M. vimineum* and *A. altissima* seed bags were buried in mid-December 2010. All species were still dispersing seeds at the time of seed bag deployment. Half of the bags were placed on more cool and mesic north-facing slopes, and half of the bags were placed on more warm and xeric south-facing slopes. Bags were placed near control sites so that the bags provide information relevant to the nearby recruitment survey. Location near controls also ensured that treatment effects did not influence seed dynamics and accidental introduction did not occur into uninvaded areas.

Seed bags were recovered at 2 month intervals for 24 months. In total, 3 species x 5 replicates x 2 slope aspects x 12 removal dates= 360 bags. The recovered seeds were tested for germination on moist filter paper in Petri dishes. Germination on filter paper implies enforced dormancy because germination occurred after entering a favorable environment without a stimulus that may break induced dormancy (such as photoperiod). Non-germination implies innate or induced dormancy because a favorable germination environment alone does not stimulate germination. Zero *A. petiolata* seeds germinated in the lab due to strict temperature fluctuations necessary for germination, a form of innate dormancy (Cindy Huebner, pers. communication). However, the number of seeds that germinated in the field was evident due to the presence of the empty seed coat, so the number of seeds that germinated in the field was used for *A. petiolata* germination data. *L. quadrifolia* was removed from the design because the embryos were too small to accurately determine viability visually and no seeds germinated in the petri dishes.

Seeds that did not germinate were tested for viability by visually observing the embryo for firmness and a yellow or green color, which indicated viability. This method that was confirmed as accurate by tetrazolium trials. Tetrazolium tests were not used throughout the study because the seeds had already imbibed water from germination testing and did not readily absorb tetrazolium solution. To confirm the visual viability method, 100 seeds from 5 random seed bags (20 seeds each) that appeared viable were cut in cross-section 1/3 the length of the seed from the base of the seed and soaked in 1% 2,3,5-triphenyl-tetrazoliumchloride solution overnight at room temperature following Huebner (2011). The seeds were sliced open the rest of the way and examined under a dissecting scope for an evenly stained embryo, which indicates viability. Unstained or splotchy embryos were considered nonviable. One hundred percent of *A. petiolata* and *A. altissima* seeds that appeared viable tested viable. Ninety-nine percent of *M. vimineum* seeds that appeared viable tested viable.

Each species' capacity for seed dormancy was estimated by expressing the number of seeds in enforced dormancy and total living seeds as a proportion of total seeds buried and plotted against time following Sarukhán (1974). To test whether proportion of seeds in enforced dormancy was affected by aspect and season, repeated measures ANOVA was performed with proportion of seeds in enforced dormancy as the repeated measure and aspect and time as factors. Repeated measures ANOVA was used because seed bags were recovered from the same 5 sites at each sampling date.

Seed mortality data was used to create survivorship curves for all species which were compared using Cox-Proportional Hazard analysis in R 2.12.1. Cox-proportional hazards designates a cumulative distribution function to time (T) that is associated with a survival function (based on proportion of surviving seeds at T). The hazard function, which expresses the risk of death at each point in time, is dependent on the survival function. To test for differences between curves, a log-likelihood ratio is generated using the hazard function and a null value. The log-likelihood ratio is compared between curves to attain a P-value (Fox 2002). Time was treated as a continuous variable and survival was treated as a dependent variable. Covariates were aspect and species, which were tested by looking for a relationship between the individual curves of each covariate and the hazard function. A test of interaction looks for a relationship between the curves of the two covariates. The test statistic is a p-value that is reached by assessing how strict is the relationship between each covariate curve and the hazard function. The interaction effect test statistic is also a p-value that based upon a relationship between the two covariates in which one covariate is higher or lower than predicted based upon the level of the other covariate. A type I survivorship curve is found if risk of death increases with age. Risk of death decreases with age in a type III survivorship curve (due to high mortality at young ages) and a for a type II survivorship curve, death is independent of age and happens consistently throughout time.

Regression was used to determine whether a relationship exists between time and log proportion seed survivorship. In the cases that a relationship was found, half-life and expected longevity of the seed bank was found by calculating y= log(50) and y=log(1).

No seed bags were deployed in the Ridge and Valley region. The Ridge and Valley region was surveyed for invasive species and population edges were marked. The number of individuals in a 1 m^2 plot within the population and adjacent to the population edge was recorded. However, this portion of the study was curtailed and no further data was collected because travel between regions was time-consuming and therefore impractical.

RESULTS

Each species showed a characteristic phenology of emergence and reproduction, repeated in 2010 and 2011. *A. petiolata* fruited in early summer, while *A. altissima* and *M. vimineum* fruited in late autumn.

Dispersal of *Alliaria petiolata*

A. petiolata showed the reproductive portion of its biennial life history in 2010 and the juvenile rosette phase in 2011. *A. petiolata* reproductive adults bolted in March 2010 and were flowering by April. Most plants had just one inflorescence but a few unusually large individuals in the study populations had up to 5 inflorescences that originated from the base of the plant. Individuals reached 1 m in height and flowers were produced on a terminal raceme. Each plant produced at least one silique, but most produced 6-10 siliques per inflorescence. Flowers persisted through May, and most plants developed siliques by early June. Some plants continued to flower in June while siliques were developing lower on the raceme. Plants set seed in late June and died by mid-July but dry siliques remained on upright stems and continued to disperse seeds until October, 2010.

The 2011 populations were almost entirely juvenile rosettes (Figure 1), with just one reproductive adult among all study populations (This adult does not appear in figure 1 because it was not on the population edge). The juvenile rosettes emerged late in March 2011 and had several leaves by May. In 2010, only adult plants were present at the edge of the populations and zero individuals (by definition) appeared in the plot outside of the populations (Figure 1). In 2011, all observed individuals were in the juvenile rosette stage, and individuals existed at a lower density outside of the population edge. Juvenile rosettes existed at higher density in 2011 than adults in 2010 in most cases. To test for several factors, a nested ANOVA test with the design: 2 treatments (control, burn) x 2 locations (inside, outside) x 2 replicate sites x 3-4 replicate transects nested within sites (Table 2) was performed. A significant difference was found between treatments (p=0.012) (Table 2). Control *A. petiolata* populations have significantly higher seedling establishment than burn plots (p=0.002), with 306% more seedlings than burn plots

Table 2

Variation in A. petiolata demography between treatments tested with a nested ANOVA.

Source of Variation	Sum Sq	Mean Sq	F value	df	P-value
Treatment	858.67	858.67	19.20621	1	0.0023410 **
Location	1377.80	1377.80	30.8176	1	0.0005401 ***
Site	1354.34	1354.34	30.2929	1	0.0005711 ***
Treatment x Location	594.07	594.07	13.2878	1	0.0065391 **
Treatment x Site	1897.79	1897.79	42.4483	1	0.0001851 ***
Location x Site	837.05	837.05	18.7226	1	0.0025223 **
Residuals	357.67	44.71		8	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

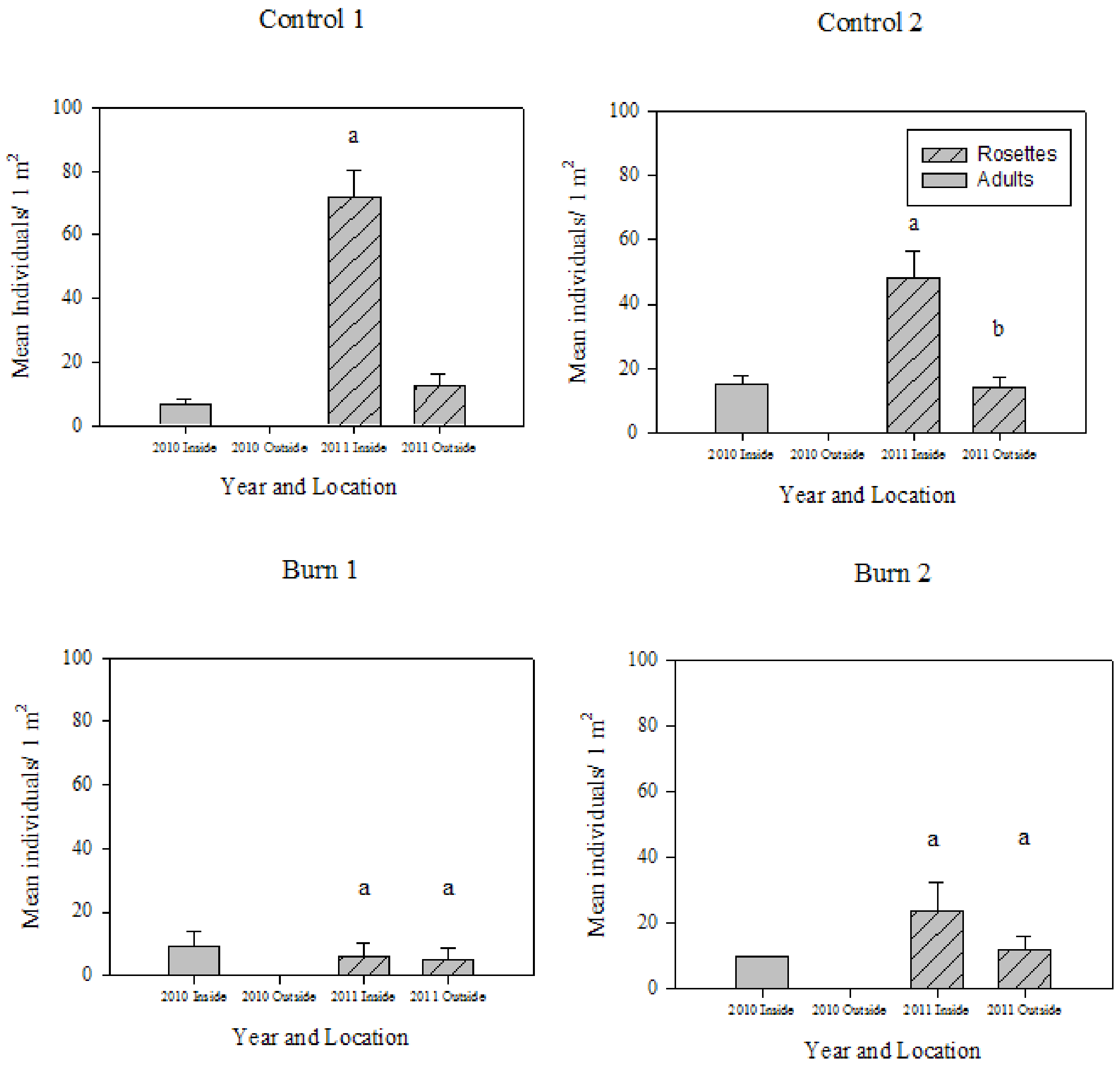


Figure 1: Stem density at the edge of *A. petiolata* study plots at four sites. Each bar represents the mean of three or four transects. "Inside" refers to the 1 m^2 plot within the population adjacent to the edge, and "outside" refers to the 1 m^2 plot adjacent to the population that was not yet colonized in 2010. Presence of juvenile rosettes in the "2011 outside" category indicate population expansion. Error bars represent one standard deviation.

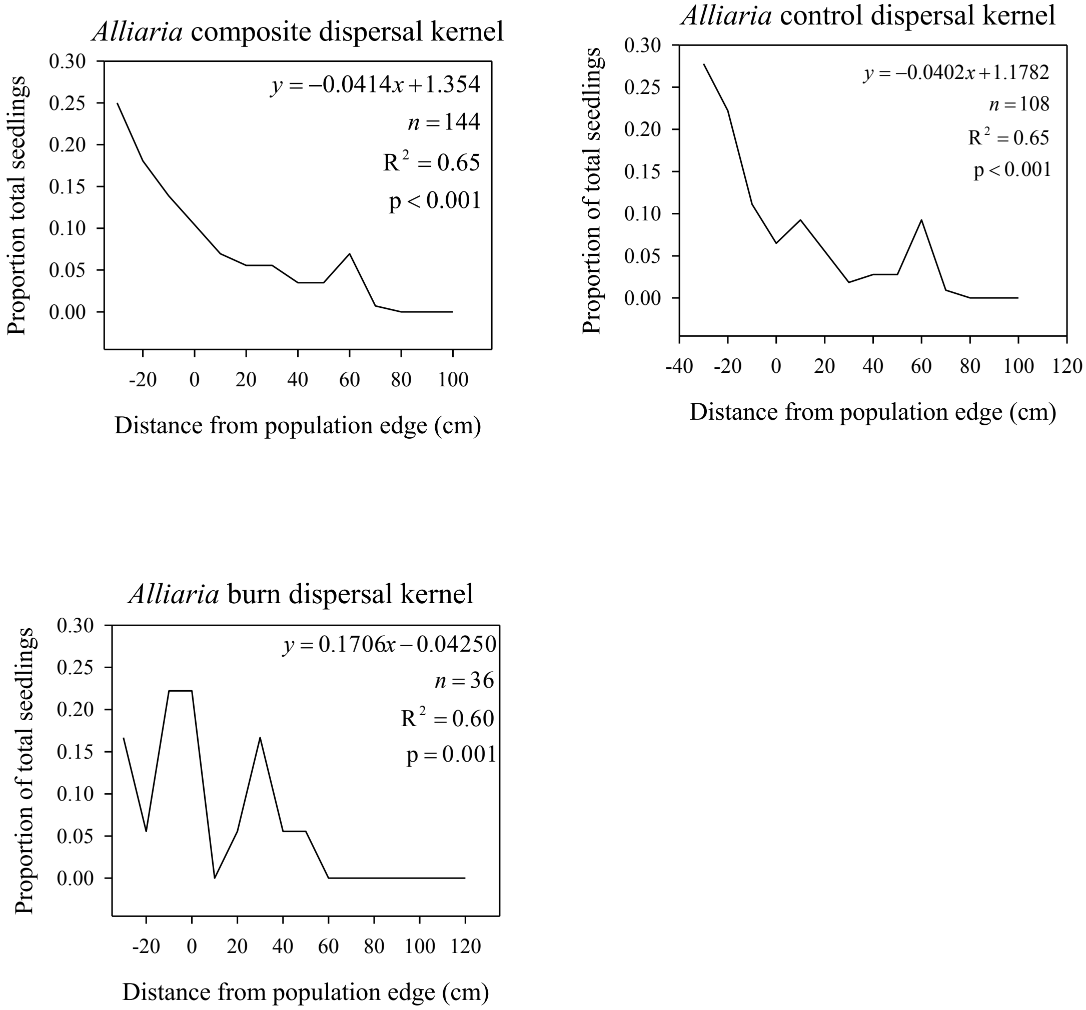


Figure 2: Decline of *A. petiolata* stems with distance from the population edge expressed in a dispersal kernel. Log frequency was regressed on distance from the population edge. The burn dispersal kernel shows the data from two sites including four replicates. The control dispersal kernel shows the data from two sites including six replicates. Composite dispersal kernel shows the combined data from control and burn sites including ten replicates. The regression equation and samples size (n) are shown on each graph. Find regression information in Table 2.

Seed bank samples showed zero emergence across all sites for *A. petiolata.* However, stratified seeds were planted in a control flat of forest soil, and zero emergence was observed, indicating that the greenhouse environment may have been unsuitable for germination. Therefore, seeds may have been present in the soil samples but did not germinate due to innate dormancy.

Few seeds were collected in *A. petiolata* seed traps, and all seeds appeared in seed traps placed 0 m, or adjacent to, the population edge. Two seeds appeared in the seed trap placed 0 m (adjacent to the population edge) from Burn 1, replicate 2, one seed appeared the seed trap 0 m from Burn 2 in replicates 1 and 2. Dispersal distance was much less than my seed trap array was designed to measure, and the numbers of trapped seeds are too low to perform regression analysis, so seedling establishment in 2011 was used to determine dispersal distance.

A. petiolata seedlings were observed to colonize a maximum 70 cm from the population edge at control site 1, 60 cm from the population edge at control site 2, and 50 cm from the population edge at burn sites 1 and 2. Log frequency was regressed on distance from the population edge, and R^2 values ranged from 0.7288 at control site 1, replicate 2 to 0.2932 at burn site 1, replicate 1 (Table 2). Dispersal curves show a significant decline of stems with distance across all replicate directional transects within sites, with the exception of two control and one burn replicates that were non-significant (Table 2).

Table 3

Dispersal in A. petiolata inferred from seedling distributions.

Treatment	Site	Replicate	intercept	slope	n	df	R^2	Adjusted R^2	F-value	P-Value
Control	1	1	0.22736	-0.03962	36	12	0.557	0.5201	15.09	0.002169
Control	1	2	-0.0428	-0.6573	37	12	0.7288	0.7062	32.25	0.000102
Control	2	1	-	-	11	-	-	-	-	n.s
Control	2	2	-1.1451	-0.03952	8	12	0.6477	0.6184	22.07	0.000516
Control	2	3	NA	NA	0	NA	NA	NA	NA	NA
Control	2	4	-	-	9	-	-	-	-	n.s.
Burn	1	1	-1.265	-0.02757	5	12	0.2932	0.2343	4.978	0.04551
Burn	1	2	NA	NA	0	NA	NA	NA	NA	NA
Burn	2	1	-	-	11	-	-	-	-	n.s
Burn	2	2	-1.413	-0.03088	9	12	0.3786	0.3268	7.331	0.01917

Dispersal of *A. petiolata* inferred from seedling distributions. The relationship between log frequency and distance from population edge for all replicates tested with regression analysis. R^2 value shows the proportion of variation attributed to the dependent variable (distance) and the adjusted R^2 shows the same proportion but is adjusted for sample size (n). The F-value compares the experimental data to the null model of uniform stem number with distance from population edge and is used to compute the p-value. Replicates that had zero recruitment (n=0) were excluded from regression analysis (NA) and were not used to estimate dispersal distance. N.s. = non-significant.

The low adjusted R^2 value in relation to the R^2 value of all three non-significant replicates suggests that the non-significance of these sites was influenced by low sample size (n); an effect of low seedling recruitment. One control replicate and one burn replicate were excluded from the test because zero recruitment was observed within or beyond the population edge in 2011. A composite graph in figure 2 shows that *A. petiolata* populations in general show a relationship between stem density and distance from the population edge ($p<0.001$). When tested separately, control treatments showed a relationship between frequency and distance from the population edge (p<0.001) and so did burn treatments (p=0.003) (Figure 2).

Table 4

Differences in A. petiolata frequency with distance from the population edge between

Source of Variation	SS	MS	F value	df	P value
Distance	141.00	141.002	44.9133	1	2.382e-10 ***
Treatment	20.40	20.397	6.4972	1	0.01161 *
Site	17.51	17.509	5.5771	1	0.01923 *
Distance x Treatment	2.11	2.113	0.6730	1	0.41307
Distance x Site	2.86	2.857	0.9100	1	0.34135
Treatment x Site	4.12	4.119	1.3121	1	0.25348
Residuals	583.93	3.139		186	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

A nested ANCOVA test comparing dispersal kernels within treatments, nested by site and replicate, showed significant difference between treatments (p=0.001) and a very strong relationship between frequency and distance (p<0.001) (Table 4).

Dispersal of *Microstegium vimineum*

M. vimineum emerged in late June and had reached maximum size by July in both 2010 and 2011. *M. vimineum* began to flower in late August and September of 2010 and 2011. Time of flowering varied by 2-3 weeks between populations. Inflorescences contained between 10 and 20 seeds. Often chasmogamous and cleistogamous flowers were present on the same inflorescence. Chasmogamous flowers existed at the top of the inflorescence, and the anthers were exposed and evident during time of flowering. Cleistogamous flowers were enclosed by a curled leaf around the base of the inflorescence, so anthers and other flower structures were not exposed at time of flowering (pers. observation). Cleistogamous flowers became evident in the fall when the enclosing leaf was removed for seed collection. Seeds were mature by mid-late October and the exposed chasmogamous seeds dispersed prior to the enclosed chasmogamous seeds. Many seeds remained attached to the adult plant throughout November, until the thatch was matted to the ground.

Soil seed bank samples indicated the presence of a seed bank for *M. vimineum* 0 m from (adjacent to) the population edge. Three seedlings emerged from the sample taken from in harvest site 1, replicate 1. The soil samples were taken after seedling emergence, so many individuals had already germinated and the minimum seed bank was sampled.

Seed collection in seed traps was limited to traps placed 0 m, adjacent to the population edge, in 2010 and 2011. Five seeds appeared in harvest site 1, replicate 1, and two seeds were found in harvest site 1, replicate 2 in 2010. Sixteen seeds appeared in harvest site 2, replicate 1, and 12 seeds appeared in harvest site 2, replicate 3 in 2010. In 2011, three seeds were found in burn site 1, replicate 2, and one seed was found in control site 2, replicate 1. Seed dispersal distance was much less than the seed trap array was designed to measure and sample size was limited, so seedling establishment data was used to estimate dispersal distance.

M. vimineum seedlings colonized a maximum of 110 cm from the population edge at control site 1, 30 cm from the population edge at control site 2, 100 cm from the population edge at burn site 1, 60 cm from the population edge at burn site 2, 40 cm from the population edge at harvest site 1, and 40 cm from the population edge at harvest site 2. Regression analysis (Table 4) showed a significant decline of stem number with distance between all replicate transects within sites.

Table 5

Dispersal of M. vimineum inferred from seedling distribution.

Treat-ment	Site	Repli-cate	intercept	slope	n	df	R^2	Adjusted R^2	F-value	P-Value
Burn	1	1	0.23553	-0.0226	35	13	0.265	0.2079	4.675	0.04984
Burn	1	2	-0.0934	-0.03679	42	13	0.483	0.4432	12.14	0.004029
Burn	2	1	-1.91	-0.0295	12	13	0.486	0.4462	12.28	0.00388
Burn	2	2	-.00411	-0.04094	9	13	0.632	0.604	22.32	0.000397
Control	1	1	-0.1408	-0.05219	60	12	0.7873	0.7696	44.42	2.311e-05
Control	1	2	-0.433	-0.0408	42	14	0.6999	0.6784	32.64	5.356e-05
Control	2	1	0.2685	-0.03704	25	14	0.5473	0.515	16.93	0.001053
Control	2	2	-0.5836	-0.0385	20	14	0.6652	0.6413	27.82	0.000118
DLC	1	1	0.51996	-0.04683	69	14	0.7914	0.7765	53.1	3.988e-06
DLC	1	2	0.09934	-0.04499	47	14	0.7704	0.754	46.97	7.894e-06
DLC	1	3	0.35696	-0.05032	76	13	0.7521	0.733	39.44	2.834e-05
SW	2	1	0.03004	-0.04646	42	13	0.7393	0.7193	36.87	3.955e-05

Dispersal of *M. vimineum* inferred from seedling distributions. The relationship between log frequency and distance from population edge for all replicates tested with regression analysis. R^2 value shows the proportion of variation attributed to the dependent variable (distance) and the adjusted R^2 shows the same proportion but is adjusted for sample size (n). The F-value compares the experimental data to the null model of uniform stem number with distance from population edge and is used to compute the p-value. DLC=Diameter-Limit Cut, SW=Shelterwood Harvest.

A nested ANCOVA tested stem density and distance as covariates, with the factors treatment, site, and replicate nested in that order. No significant difference was found between treatments but a very strong relationship existed between stem number and distance from the population edge (Table 5).

Table 6

Factors influencing frequency in M. vimineum populations

Source of Variation	SS	MS	F value	df	P value
Distance	623.02	623.02	297.7778	1	< 2.2e-16 ***
Treatment	1.80	0.90	0.4291	2	0.651744
Site	16.30	16.30	7.7890	1	0.005834 **
Distance x Treatment	12.36	6.18	2.9549	2	0.054657
Distance x Site	0.13	0.13	0.0620	1	0.803656
Treatment x Site	7.34	3.67	1.7543	2	0.176025
Residuals	370.33	2.09		177	

Factors influencing frequency in *M. vimineum* populations. Differences in frequency with distance from the population edge between treatments tested with a nested ANCOVA. Significance codes : 0 '***' 0.001 '**' 0.01 '*' 0.05.

ANCOVA testing stem density and distance as covariates with treatment, site, and replicate nested in that order showed no significant difference between treatments, which suggests that the same mechanism controls dispersal among treatments, therefore sites were combined (Table 6) (Figure 3). Each treatment showed a decline of stem density with distance from the population edge (Figure 3) (Table 6).

Table 7

Dispersal of M. vimineum inferred from seedling distributions.

Species	Treatment	intercept	Slope	n	df	R^2	adjR^2	F-value	P-value
MV	Control	.71296	-0.04232	170	14	0.6027	.5744	21.24	0.0004055
MV	Burn	.87901	-0.03459	120	14	.4935	.4573	13.64	.002409
MV	Harvest	1.0828	-0.0555	234	13	0.7946	0.7788	50.3	8.146e-06
MV	Composite	1.5064	-.02971	524	14	0.4178	.3762	10.05	.006822

Dispersal of *M. vimineum* inferred from seedling distributions. The relationship between distance and log frequency among treatments is tested by regression analysis. Each of these regressions shows several sites and replicates lumped by treatment. “Composite” refers to lumped regression including all replicates of *M. vimineum*. R^2 value shows the proportion of variation attributed to the dependent variable (distance) and the adjusted R^2 shows the same proportion but is adjusted for sample size (n). The F-value compares the experimental data to the null model of uniform stem number with distance from population edge and is used to compute the p-value.

Treatments were pooled to create one composite *M. vimineum* dispersal kernel (Figure 3) which illustrates the clear and significant (p=0.0068) decline of stem number with distance from population edge.

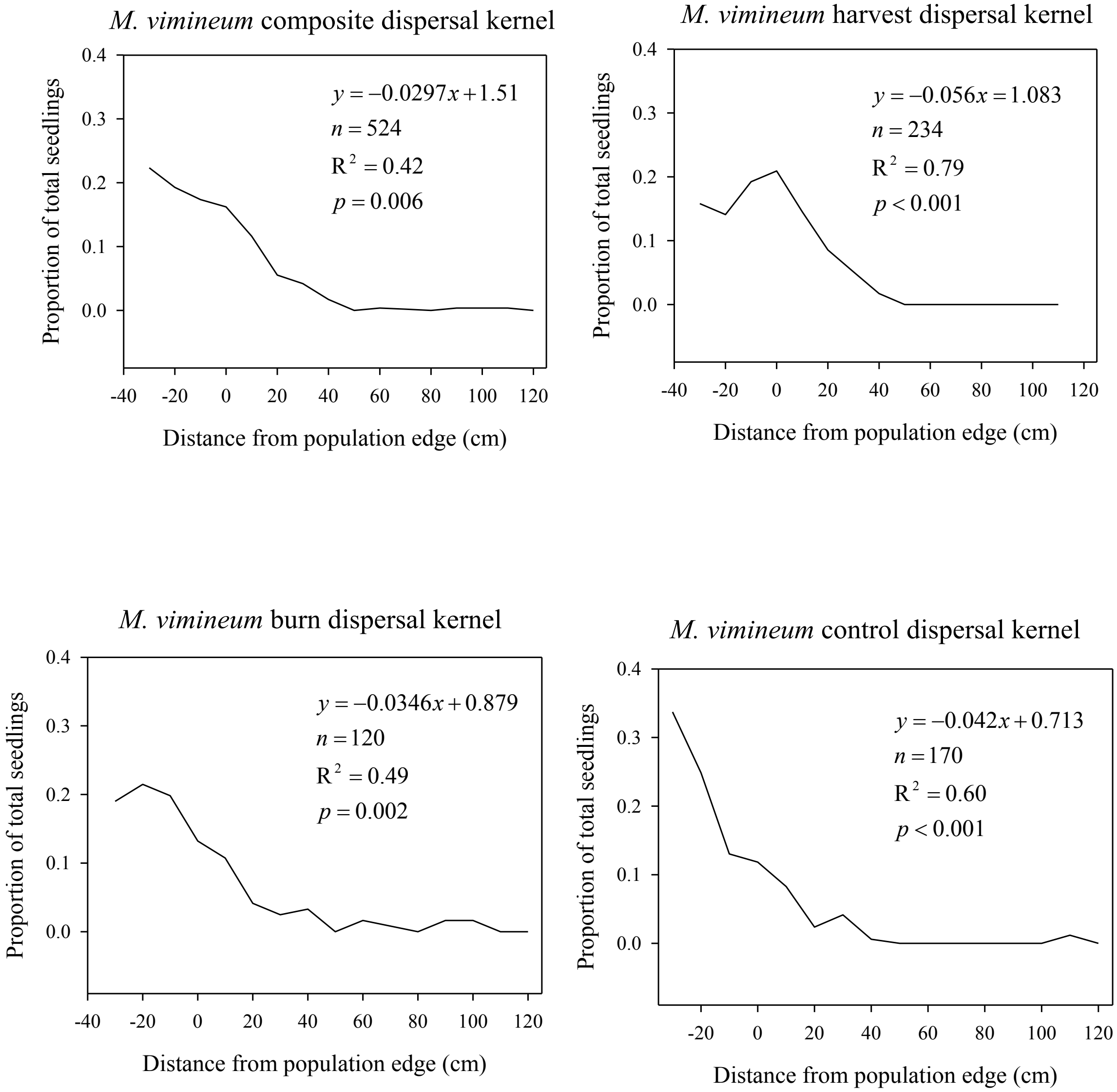


Figure 3: *M. vimineum* dispersal inferred from seedling establishment. Proportion of total seedlings on the y axis is plotted against distance from the population edge on the x axis to show the relative number of seedlings at each sampling distance. Log frequency was regressed on distance from the population edge (Table 6) to show the rate of seedling decline with distance from the population edge. The equations represent the regression line associated with each graph and n is the sample size (number of seedlings observed).

Dispersal of *Ailanthus altissima*

Soil seed bank samples found zero seedling emergence. However, these negative results cannot be used to infer that *A. altissima* does not form a seed bank because the data are not replicated.

Collection of seeds in seed traps for *A. altissima* was not observed (zero seeds collected), and zero seedling emergence was observed in the experimental plots or in the surrounding area. Therefore, dispersal distance for *A. altissima* was not quantified in this study. The closed canopy condition of the site may have been preventing further establishment. Since just one site was sampled for *A. altissima,* stochastic variation had a strong effect on the results, so these negative results cannot be used to infer lack of dispersal and spread for the species.

Dormancy Condition

Enforced dormancy tests examined the proportion of seeds enter each state of dormancy for each species, and whether dormancy is affected by time and slope aspect. “Induced” refers to seeds that did not readily germinate although they were viable, suggesting a state of induced dormancy. “Enforced” refers to seeds that germinated on filter paper in petri dishes in the lab, which implies enforced dormancy was taking place in the field. “Nonviable” seeds did not have a viable embryo, usually because the seed had germinated before sampling but sometimes the seed had rotted or molded. The cause of non-viability was unclear for most species so non-viable seeds were treated as one measure for all species except *A. petiolata,* which has a hard shell-like seed coat that remains after the embryo has germinated. Therefore, non-viable seeds observed in *A.*

petiolata seed bags were categorized as “Nonviable embryo” and “nonviable (germinated)” based upon the presence or absence of a rotten embryo in the seed coat. The number of non-viable seeds is taken from a different seed bag at each date, so mortality is not cumulative: mortality appears to increase and decrease on the graphs due to stochastic variation between seed bags at each sampling date.

Microstegium vimineum seeds showed very high enforced dormancy and survivorship at the beginning of the study but survivorship dropped to only 10-20% after six months. Initially, germinable seeds (enforced dormancy) existed in a much higher proportion than dormant seeds (induced dormancy) but seeds experiencing induced dormancy exist in a higher proportion than seeds experiencing enforced dormancy after the 80-90% mortality that occurs after six months (Figure 4). The proportion of seeds experiencing induced dormancy relative to seeds in both the nonviable and enforced dormancy categories remains relatively consists at 10-15% on north-facing slopes. Cox-Proportional Hazards Model analysis showed that enforced dormancy varied between slope aspects for *M. vimineum* (p<0.001) (Table 8).

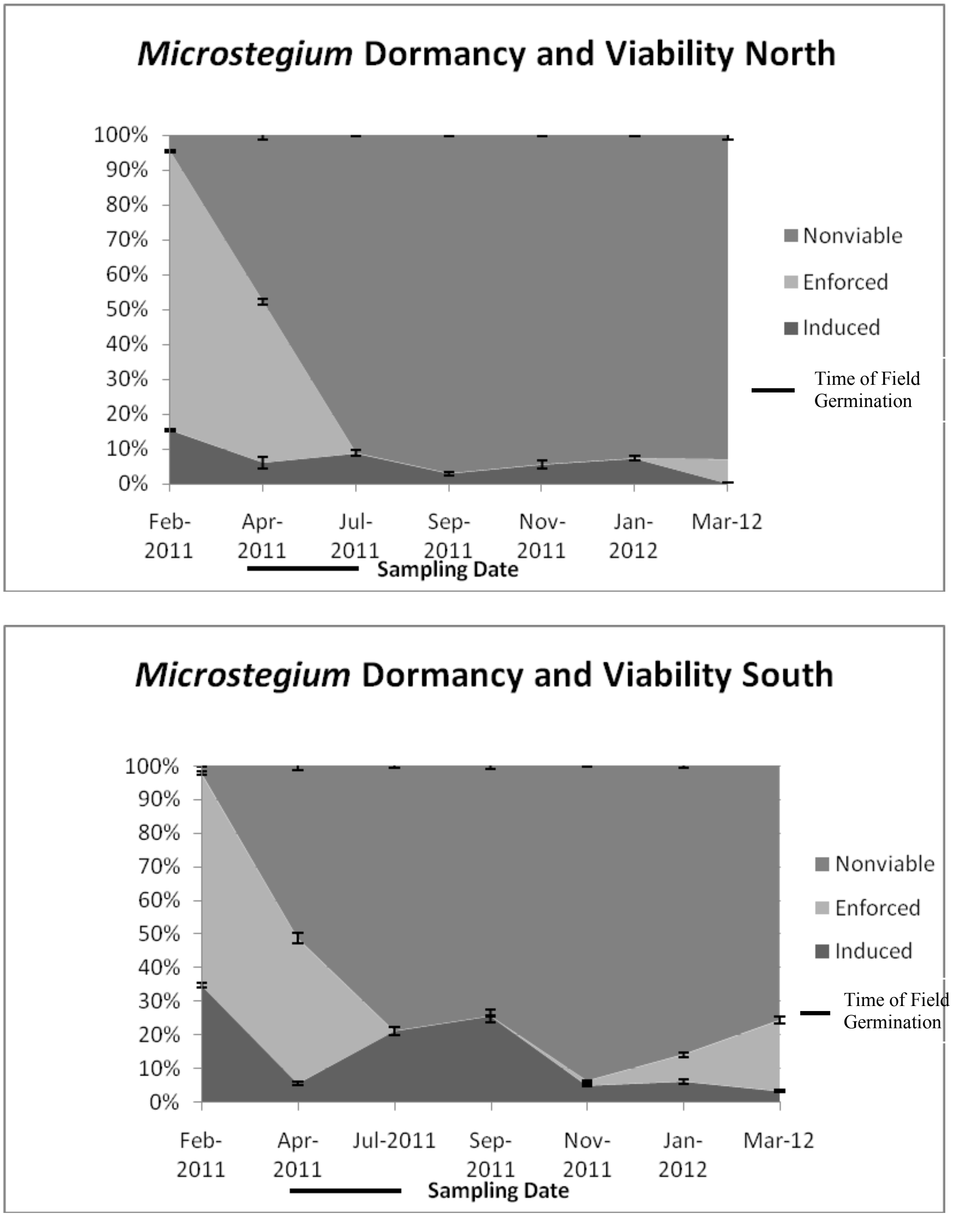


Figure 4: Dormancy condition of *M. vimineum* on two slope aspects. The effect of slope aspect on enforced dormancy was significant ($p<0.001$). Proportion of total seeds in the state of enforced or induced dormancy, and nonviable is shown. North and south-facing slopes are each represented by 3-5 replicate seed bags, to account for the effect of spatial environmental heterogeneity. The error bars show ±1 standard error.

Table 8

Differences in dormancy condition on north and south-facing aspects.

Subject	Source of Variation	df	n	Log-Likelihood Ratio	p-value
A. petiolata	aspect	1	7372	57.6	1.8e-13
M. vimineum	aspect	1	3146	11.4	0.00074
A. altissima	aspect	1	4869	31.8	1.9e-08
A. saccharum	aspect	1	3136	7.83	0.0051
E. rugosum	aspect	1	6496	72	0.000000

Differences in dormancy condition on north and south-facing aspects. Cox-Proportional Hazards Model analyses summary table showing the results of five separate within-subject tests assessing the effect of slope aspect on seed enforced dormancy. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value.

M. vimineum experienced 16% higher enforced dormancy on north-facing aspects than south-facing aspects in February 2011, and north-facing slopes experienced 0% enforced dormancy in January 2012 while south-facing slopes experienced 8% enforced dormancy with a comparable proportion of viable seeds (Figure 4). The narrow range of the error bars show that this trend is relatively consistent among replicate bags. Time was found to be a significant factor affecting germination ($p<0.001$), which suggests that enforced dormancy occurs seasonally. The greatest enforced dormancy was seen in February 2011 and the least enforced dormancy was seen in summer and fall of 2011. Regression found no relationship between seed survivorship and time on north or south-facing slopes.

Ailanthus altissima experienced enforced dormancy of 50-90% in the first two months which was followed by a six-month period of zero enforced dormancy (Figure 5), although about 50% of the seeds remained viable and about 50% were in a state of induced dormancy. A slight rise in enforced dormancy was seen in January 2012 and a dramatic rise in enforced dormancy was seen in March 2012, which corresponds to the natural germination period of *A. altissima*. Germination was found to be different between slope aspects for *A. altissima* ($p<0.001$) (Table 8). *A. altissima* experienced 23.6% higher germination on north-facing slopes compared to south-facing slopes in April 2011 and 11% higher germination on north-facing slopes than south-facing slopes in September 2011 (Figure 5). The narrow range of the error bars show that these trends were consistent among replicates. Time was found to be a significant factor affecting enforced dormancy ($p<0.001$), which suggests that enforced dormancy is affected by season. The highest enforced dormancy was seen in April 2011 and the least enforced dormancy was seen in summer and fall of 2011. Regression found a relationship between seed survivorship and time on north and south-facing slopes (Table 8).

Table 9

Seed survivorship of A. altissima seeds found from analysis of buried seed bags at different points in time.

Species	Aspect	Intercept	Slope	n	df	R^2	adjR^2	F-value	P-value
AA	north	2.0028	-0.0257	27	26	0.341	0.3156	13.45	0.001105
AA	south	1.99854	-0.03374	29	28	0.293	0.2678	11.61	0.002007

Seed survivorship of *A. altissima* seeds found from analysis of buried seed bags at different points in time. Regression is used to find a relationship between seed survivorship and time. R^2 values show that <1% variability in survivorship can be predicted from time since seed bag burial. AA= *A. altissima.*

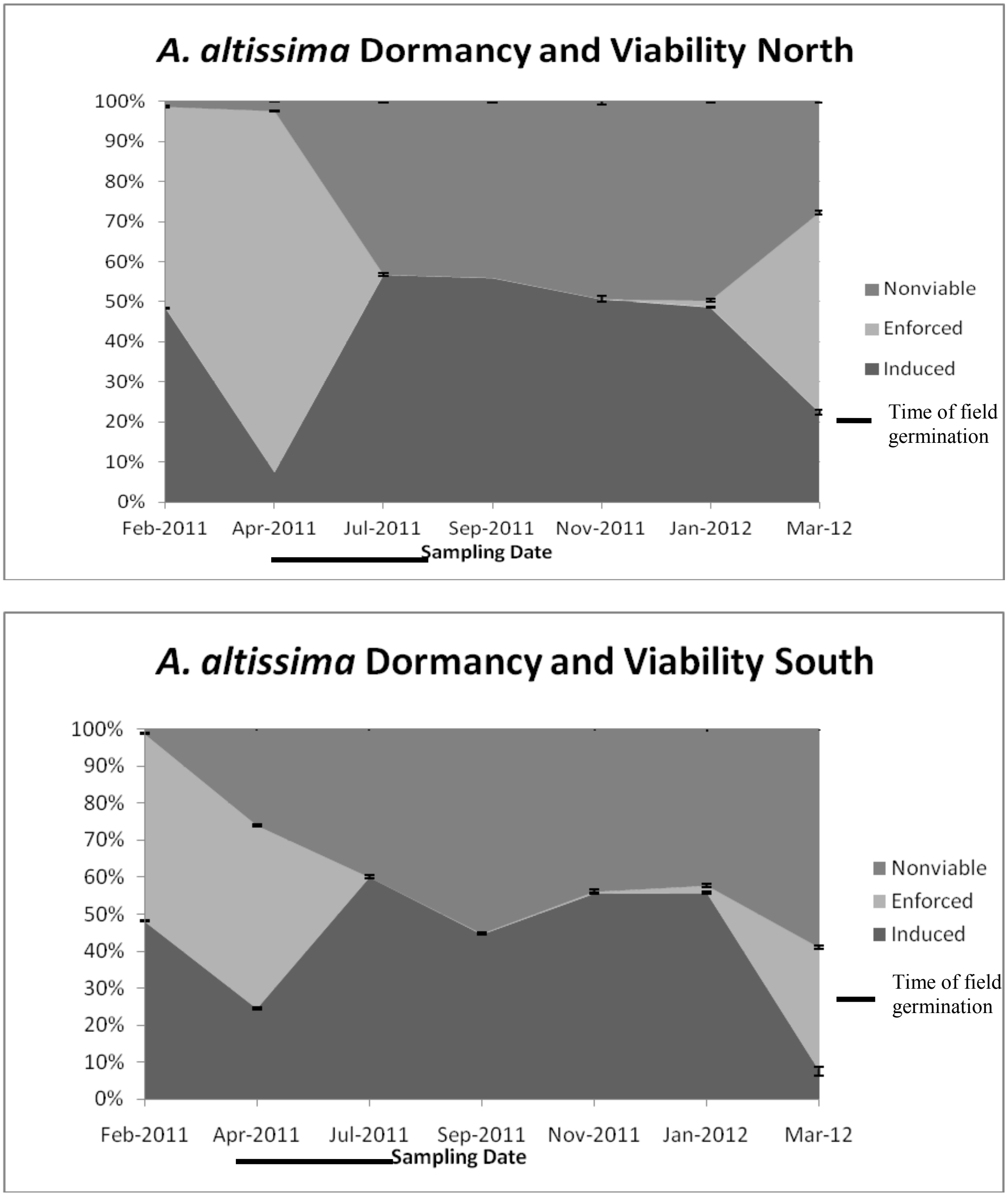


Figure 5: Changes in *A. altissima* dormancy condition through time. The effect of aspect on enforced dormancy was significant ($P<0.001$). Shaded areas show the amount of seeds in each class as a proportion of total seeds in all bags. North and south-facing slopes are each represented by 3-5 replicate seed bags, to account for the effect of spatial environmental heterogeneity. The error bars show ±1 standard error.

A. saccharum had very high initial enforced dormancy, in which 50-60% of seeds germinated, 40-30% of seeds were in a state of induced dormancy, and 5-8% of seeds were non-viable. A sudden rise in mortality was seen at 4 and 6 months, and 100% of seeds were non-viable at 8 months. No viable seeds have been found in seed bags since that date. Cox-Proportional Hazards Model Analysis showed that aspect had a significant effect on enforced dormancy ($p=0.005$) (Table 8). *A. saccharum* showed 6% higher enforced dormancy on north-facing slopes than south-facing slopes in February 2011 (Figure 6). Narrow error bars show that this trend is consistent among replicates. Time was found to affect germination ($p<0.001$) which suggests that enforced dormancy occurs seasonally. The greatest enforced dormancy was seen in February 2011, and zero enforced dormancy was seen by August 2011. Regression found a relationship between seed survivorship and time on north and south-facing slopes (Table 9).

Table 10

Viability of Acer saccharum seeds found from analysis of buried seed bags at different points in time.

Species	Aspect	Intercept	Slope	n	df	R^2	adjR^2	F-value	P-value
AS	north	1.7920	-0.5161	26	25	0.6892	0.6768	55.45	8.468e-08
AS	south	1.6308	-0.5006	29	28	0.6314	0.6182	47.96	1.578e-07

Viability of *Acer saccharum* seeds found from analysis of buried seed bags at different points in time. Regression is used to find a relationship between seed survivorship and time. R^2 values show that <1% variability in survivorship can be predicted from time since seed bag burial. AS= *A. saccharum.*

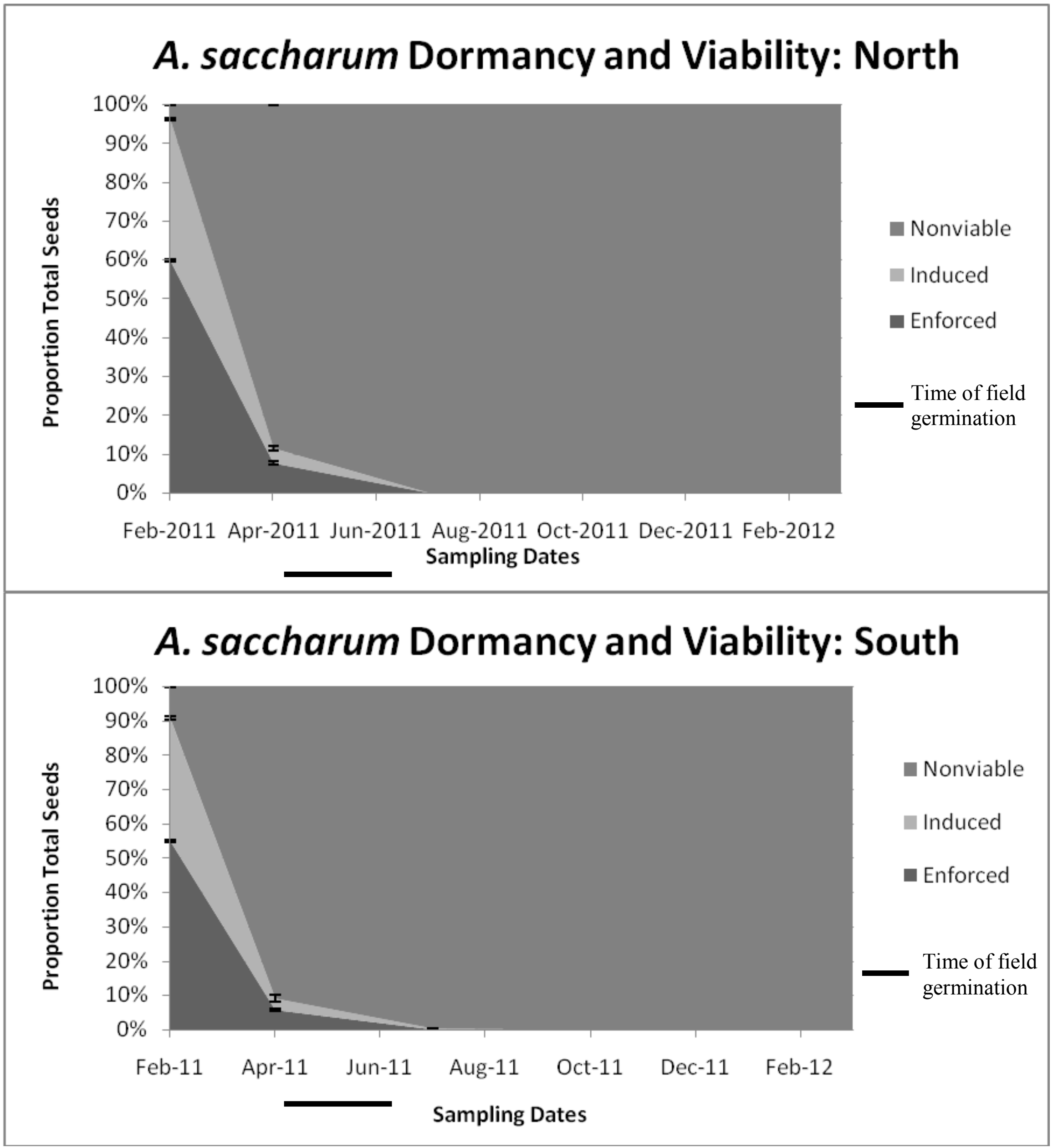


Figure 6: Changes in dormancy condition of *A. saccharum* through time. The effect of aspect on enforced dormancy was significant (P<0.001). Shaded areas show the amount of seeds in each class as a proportion of total seeds in all bags. North and south-facing slopes are each represented by 3-5 replicate seed bags, to account for the effect of spatial environmental heterogeneity. The error bars show ±1 standard error.

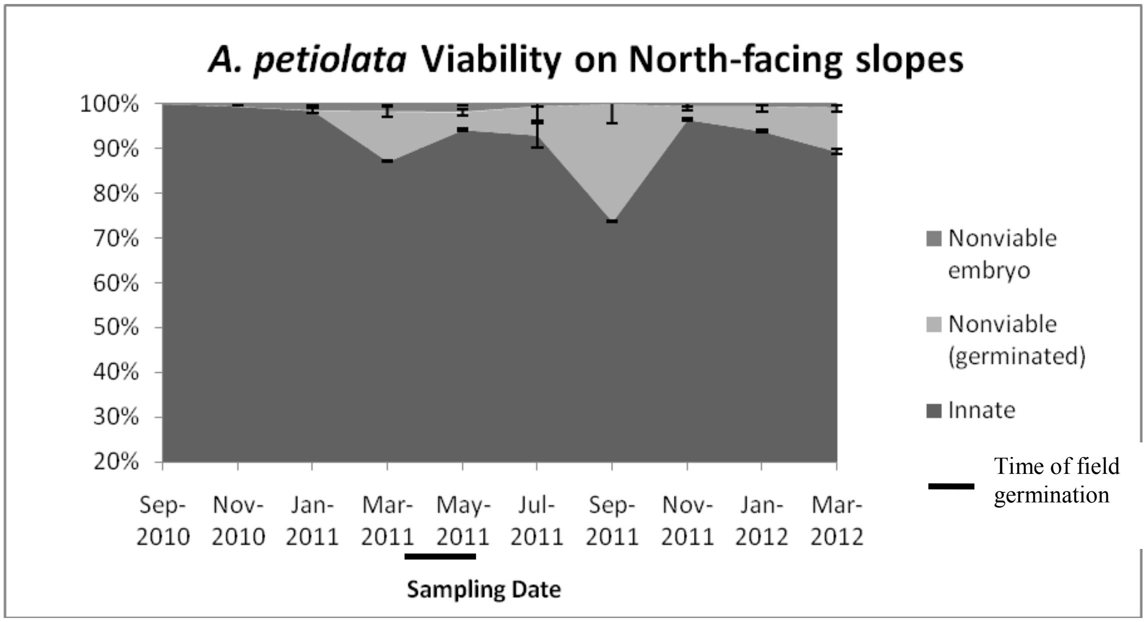
A. petiolata showed zero enforced dormancy in the lab at any date despite live embryos, probably due to innate dormancy (Huebner, pers. communication). Field germination data was recorded instead, which was found by recording the number of seeds that had germinated when the bags were opened. *A. petiolata* seeds have a hard, shell-like seed coat that persists after the young plant has died, and this seed coat is easy to distinguish from non-viable seeds that never germinated and still contain a rotten embryo inside the seed. Slope aspect was found to have an effect on *A. petiolata* field germination ($p<0.001$) (Table 8). *A. petiolata* exhibited higher field germination on north-facing slopes compared to south-facing slopes in March 2011 (10% higher) September 2011 (24%) and November 2011 (7%) (Figure 7). However, the large reach of the error bars show that this variation was inconsistent and a few sites experienced much higher and much lower germination than the mean (Figure 7). Cox-proportional Hazards Model analysis found that time affects dormancy condition of *A. petiolata* ($p<0.01$) which suggests that field germination is seasonal. The greatest field germination was observed in spring and fall 2011 and the least germination was seen in fall 2010. Regression found a relationship between seed survivorship and time on south-facing slopes but not north-facing slopes (Table 10).

Table 11

Viability of A. petiolata seeds found from analysis of buried seed bags at different points in time.

Aspect	Intercept	Slope	n	df	R^2	adjR^2	F-value	P-value
north	-	-	43	-	-	-	-	ns
south	2.009170	-0.00279	45	44	0.2426	0.2253	14.09	0.0005074

Variability of *A. petiolata* seeds found from analysis of buried seed bags at different points in time. Regression is used to find a relationship between seed survivorship and time. R^2 values show that <1% variability in survivorship can be predicted from time since seed bag burial. AP= *A. petiolata.*



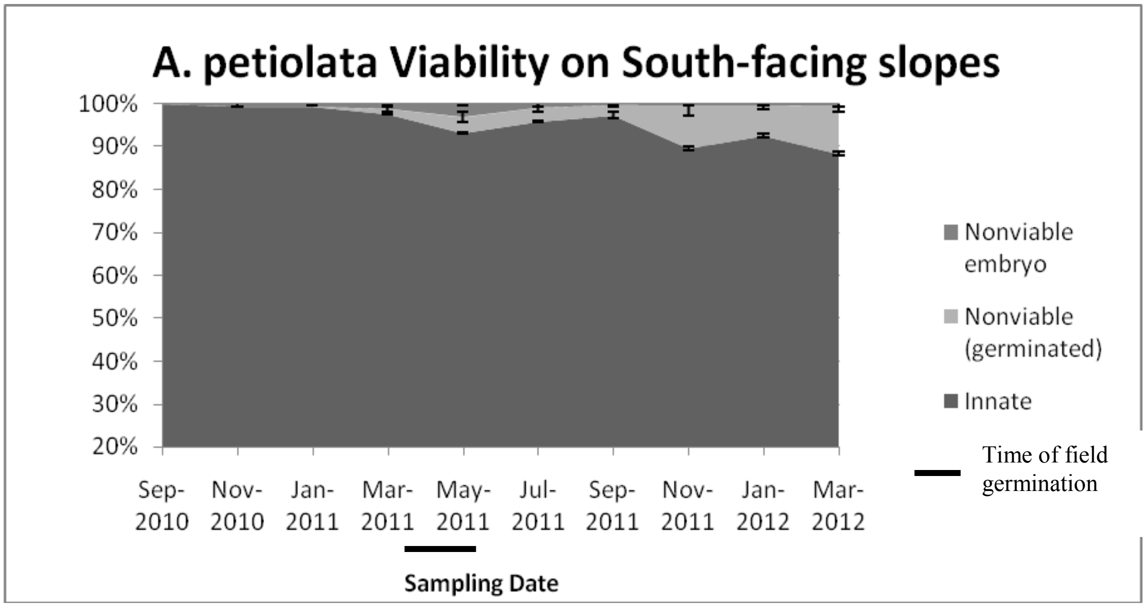
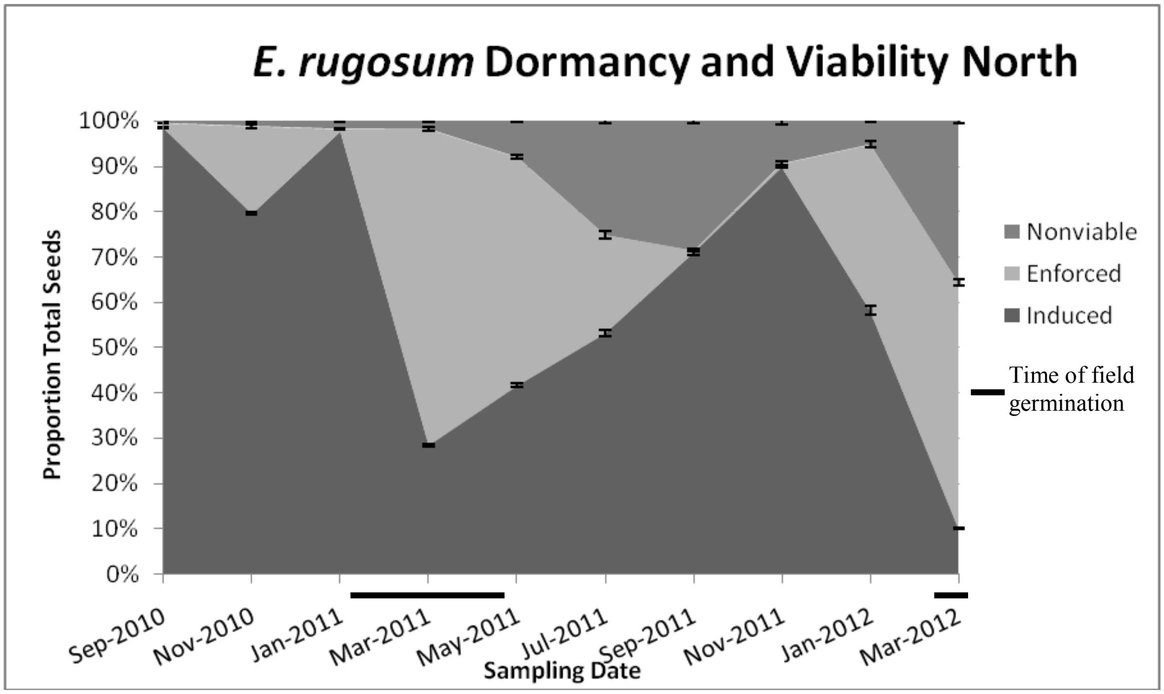


Figure 7: Changes in the dormancy condition of *A petiolata* through time. Shaded areas show the amount of seeds in each class as a proportion of total seeds in all bags. North and south-facing slopes are each represented by 3-5 replicate seed bags, to account for the effect of spatial environmental heterogeneity. The error bars show ±1 standard error. The effect of aspect on germination was non-significant for *A. petiolata* (P=0.1961). Graphs distinguish between seeds that were non-viable because they had germinated in the field (“Germinated”) and seeds that contained a non-viable embryo.

Slope aspect was found to have a significant effect on *E. rugosum* enforced dormancy (Table 8). *E. rugosum* showed higher lab enforced dormancy on north-facing slopes compared to south-facing slopes in November 2011 (14%), March 2011 (18%), May 2011 (11%), and January 2012 (13%) (Figure 8). *E. rugosum* experienced 14% higher germination on south-facing slopes compared to north-facing slopes in July, 2011. Time was found to have no significant effect on *E. rugosum* enforced dormancy but a trend of low enforced dormancy during fall 2010 and 2011 and high enforced dormancy during summer 2011 and spring 2012 is seen (Figure 8).



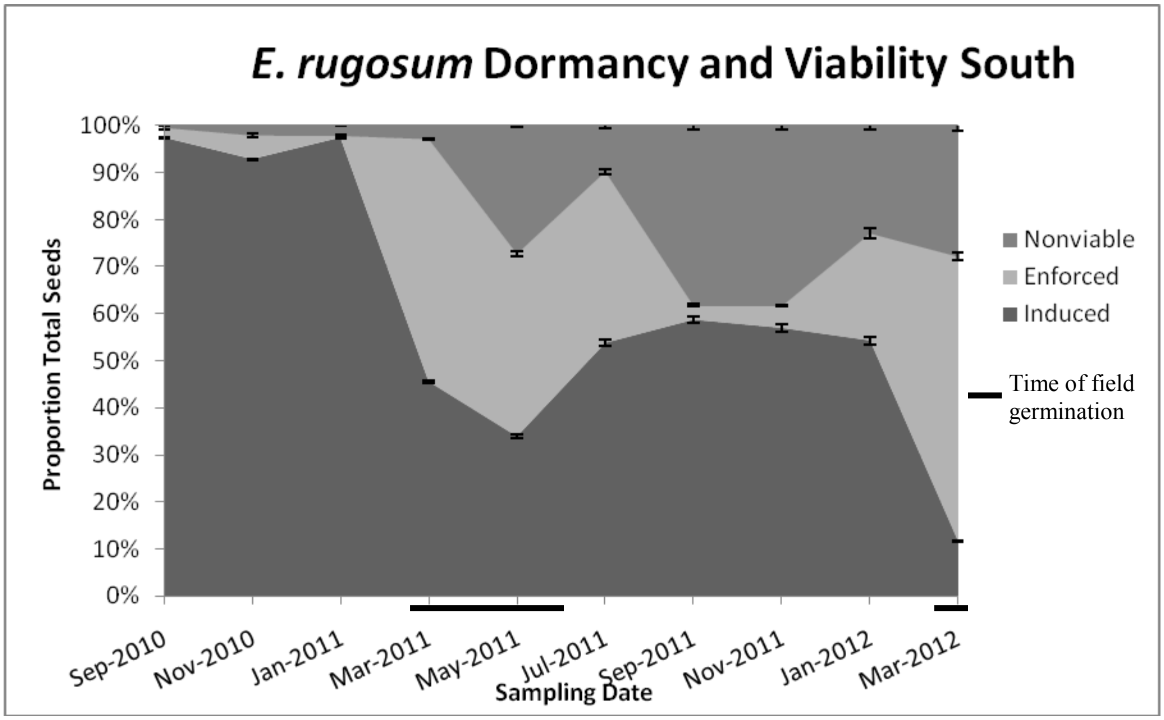


Figure 8: Changes in dormancy condition of *E. rugosum* through time. Shaded areas show the amount of seeds in each class as a proportion of total seeds in all bags. The error bars show ±1 standard error. The effect of aspect on germination was significant for *E. rugosum* ($p<0.001$).

A between-subjects Cox-Proportional Hazards Model test showed that enforced dormancy varied between invasive species, between aspects, and a species x aspect interaction was found (Table 8).

Table 12

Variability in invasive species enforced dormancy.

Subject	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AP, MV, AA	aspect	3	15387	1422	1.2e-07
	species	3	15387	1422	0.000000
	aspect x species	3	15387	1422	1.3e-02

Variability in invasive species enforced dormancy tested via between-subjects Cox-Proportional Hazards model analysis. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value AP=*A. petiolata,* MV= *M. vimineum,* AA= *A. altissima.*

Pairwise comparisons were made between invasive species to find the source of variation described by the between-subjects comparison (Table 9). It is found that the germination pattern of *A. petiolata* is significantly different from *M. vimineum* (p<0.0001) and *A. altissima* (p<0.0001). However, *M. vimineum* and *A. altissima* are seen to have no significant difference between enforced dormancy behaviors. *A. petiolata* had much lower germination than the other two species with a high of 23% germination in September 2011 on north-facing slopes. *M. vimineum* and *A. altissima* both had high germination (50-90%) in the first four months followed by <5% germination in any following month.

Table 13

Variation in invasive species enforced dormancy analyzed with pairwise comparisons.

Subjects	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AP, MV	aspect	3	10518	1476	3.9e-09
	species	3	10518	1476	0.000
	aspect x species	3	10518	1476	1.7e-05
AP, AA	aspect	3	12241	1670	1.4e-09
	species	3	12241	1670	0.00000
	aspect x species	3	12241	1670	2.2e-04
MV, AA	aspect	3	8015	43.1	ns
	species	3	8015	43.1	ns
	aspect x species	3	8015	43.1	ns

Variation in invasive species enforced dormancy analyzed with pairwise comparisons and Cox-Proportional Hazards Model analysis. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value. AP=*A. petiolata,* MV= *M. vimineum,* AA= *A. altissima.*

Pairwise comparisons are made between invasive species and the native species (Table 10). *A. altissima* and *A. saccharum* are found to have different germination patterns between species and between aspects, although no aspect x species interaction is found, which indicates that *A. saccharum* and *A. altissima* enforced dormancy is affected by slope in a similar way. *A. petiolata* and *E. rugosum* were found to have different enforced dormancy between species and aspects, and a species x aspect interaction term was found to be significant, which indicates slope affects the enforced dormancy of *A. petiolata* and *E. rugosum* differently.

Table 14

Variation between native and invasive species enforced dormancy.

Subjects	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AA, AS	aspect	3	8005	1476	0.043
	species	3	8005	1476	0.0021
	aspect x species	3	8005	1476	ns
AP, ER	aspect	3	13868	1171	2.8e-09
	species	3	13868	1171	2.0e-12
	aspect x species	3	13868	1171	1.0e-02

Variation between native and invasive species enforced dormancy compared with Cox-Proportional Hazards Model analysis. The log-likelihood ratio is the likelihood that the experimental data matches the null model. The log-likelihood ratio is used to compute the p-value. Please note that *A. petiolata* germination information comes from seeds that had germinated in the field, as no germination was observed in the lab. AA=*A. altissima,* AS=*A. saccharum,* AP=*A. petiolata,* and ER=*E. rugosum.*

Seed Survivorship

Mortality differed between species and aspects. Mortality is a measure of the number of non-viable seeds counted in each seed bag recovered. For this measurement, seeds in any state of dormancy are used to determine survivorship and seeds that are dead for any reason are used to determine mortality. These measures are different from the germination values because “Induced” and “Enforced” seeds are lumped into one measure: “viable” seeds. Non-viable measures are the same for each species except for *A. petiolata*, in which case “Nonviable embryo” and “Nonviable (germinated)” are lumped into one “nonviable” value. Each measurement is taken from different seed bags, so mortality is not a cumulative value. Survival appears to increase in some areas, but this is stochastic variation in mortality among seed bags.

A within-subject Cox-Proportional Hazards model analysis was performed on each species separately to compare survivorship on north vs. south-facing slopes (Figure 9, Table 12). *A. petiolata* survivorship on north-facing slopes was significantly different from survivorship on south-facing slopes (P=0.0014). *M. vimineum* and *A. altissima* survivorship did not significantly differ depending on slope aspect (Table 11). *E. rugosum* had significantly different survivorship on north-facing slopes than south-facing slopes (P<0.001) and so did *A. saccharum* (P<0.001, Figure 9).

Table 15

Variation in mortality between aspects.

Subject	Source of Variation	df	n	Log-Likelihood Ratio	p-value
A. petiolata	aspect	1	1799	10.9	0.0014
M. vimineum	aspect	1	1198	3.29	ns
A. altissima	aspect	1	1199	1.85	ns
E. rugosum	aspect	1	6385	23.2	2.6e-06
A. saccharum	aspect	1	3068	14.3	0.00017

Variation in mortality between aspects for *A. petiolata, M. vimineum, A. altissima, E. rugosum,* and *A. saccharum*. This table shows the summary of five separate within-subject Cox-Proportional Hazards Model analyses. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value.

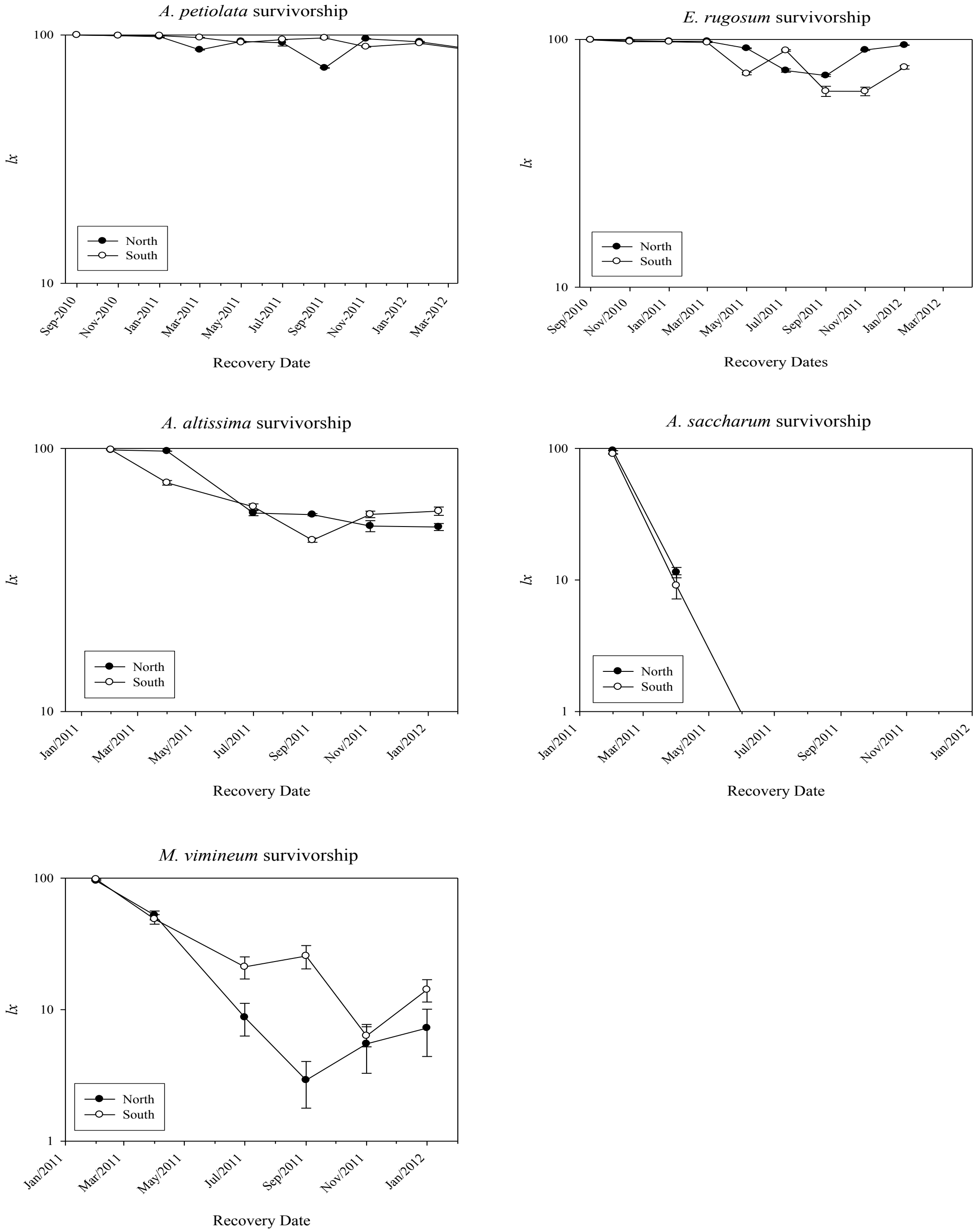


Figure 9: Survivorship of each species expressed with log-proportion surviving seed (*lx*) on the y-axis and each date of seed bag recovery on the x-axis. Each graph shows two survivorship curves; survivorship on north-facing slopes (solid points) and survivorship on south-facing slopes (white points). Please note that *M. vimineum* and *A. saccharum* graphs are set on a 1-100 scale, while the other graphs are set on a 10-100 scale to show variation on a finer scale.

A between-subjects Cox Proportional Hazards model analysis was performed with *M. vimineum, A. altissima,* and *A. petiolata* as subjects (Table 12). Significantly different survivorship by species (P<0.001) was found. *A. petiolata* appears to have a Type I survivorship curve in which there was little mortality early in the curve. At 20 months, 93% of *A. petiolata* seeds were still viable. *A.* altissima appears to have a type II survivorship curve which is characterized by steady mortality throughout time. At 12 months 52% of *A. altissima* seeds remained viable. The survivorship curve of *M. vimineum* is most like a type III survivorship curve, in which mortality is most common early in time. After 12 months only 10% of *M. vimineum* seeds remained viable. North or south aspect was found to have an effect on survivorship between subjects (p<0.001) and a species x aspect interaction was found (P<0.001).

Table 16

Variation in survivorship between invasive species.

Subjects	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AP, MV, AA	aspect	3	15220	2613	0.00073
	species	3	15220	2613	0.00000
	aspect x species	3	15220	2613	0.00077

Variation in survivorship between invasive species. Summary table of one between-subjects Cox-Proportional Hazards Model analysis of survivorship. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value. Subjects are: MV=*M. vimineum,* AP= *A. petiolata,* AA= *A. altissima.*

The between-subject Cox-Proportional Hazards Model test revealed a significant difference between species, so pairwise comparisons were made among invasive species to test for a difference between each pair (Table 13). Pairwise comparisons showed a species x aspect interaction for the pair *A. altissima* and *A. petiolata* (p<0.001). A species: aspect interaction was found for *A. petiolata* and *M. vimineum* (p<0.001) and no species x aspect interaction was found between *M. vimineum* and *A. altissima*.

Table 17

Variation in survivorship between paired invasive species.

Subjects	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AP, MV	aspect	3	10807	5306	0.012
	species	3	10807	5306	0.000
	aspect x species	3	10807	5306	0.16
AP, AA	aspect	3	11926	2689	9.4e-05
	species	3	11926	2689	0.00000
	aspect x species	3	11926	2689	2.1e-05
MV, AA	aspect	3	7707	581	3.4e-08
	species	3	7707	581	0.00000
	aspect x species	3	7707	581	3.5e-07

Variation in survivorship between invasive species. Summary table of pairwise Cox-Proportional Hazards Model analysis between invasive species survivorship. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value. MV=*M. vimineum,* AP= *A. petiolata,* AA= *A. altissima.*

Cox-proportional hazard tests between native and invasive species showed significant differences (Table 14). *A. petiolata* and *E. rugosum* differed by aspect (P<0.001), species (P<0.001), and a species x aspect interaction was found (P<0.001). *A* *petiolata* has higher survivorship at 20 months with 93% viability compared to *E. rugosum* which has 85%. However, the *E. rugosum* curve also resembles a type I curve. *A. altissima* and *A. saccharum* differed by aspect (P<0.001), species (P<0.001) and an aspect x species interaction was found (P<0.001). *A. altissima* had much higher survivorship with 54% viability at 12 months compared to *A. saccharum* that had 0% viability at 12 months (and had shown <99% viability since 6 months) which is an example of a Type III survivorship curve.

Table 18

Variation in survivorship between native and invasive species.

Subjects	Source of Variation	df	n	Log-Likelihood Ratio	p-value
AA, AS	aspect	3	7079	844	0.00000
	species	3	7079	844	0.00000
	aspect x species	3	7079	844	1.1e-16
AP, ER	aspect	3	13898	381	2.0e-06
	species	3	13898	381	4.2e-1
	aspect x species	3	13898	381	1.0e-09

Variation in survivorship between native and invasive species. Summary of Cox-Proportional Hazards Model analysis pairwise comparisons. The log-likelihood ratio is the likelihood that the experimental data matches the null model of no difference between curves. The log-likelihood ratio is used to compute the p-value. AA= *A. altissima,* AS= *A. saccharum,* AP= *A. petiolata,* ER= *E. rugosum.*

If *E. rugosum* seed survivorship continues at the observed rates, the seed bank will survive for 18 years on north-facing slopes and 9 years on south-facing slopes and have a half-life of 3 years on north-facing slopes and 1.6 years on south-facing slopes.

DISCUSSION

Invasive species spread is of primary concern in managed forests because invasive species have been shown to interfere with native woody seedling survival (Meekins and McCarthy 1999; Call and Nilson 2005; Marshall et al. 2009, Flory and Clay 2010) which may compromise tree regeneration. Invasive spread may be facilitated by prescribed burning and selective timber harvests, which are used to promote oak seedling recruitment (Abrams, 1992, 1998, 2003; Lorimer et al., 1994; Sutherland et al., 2003) but may promote invasion and therefore impede forest regeneration.

Growth, reproduction, and dispersal are small-scale demographic processes that affect a large-scale invasion. Measuring demographic variation among invasive populations informs about the effect of silviculture treatment on invasive species population expansion.

Dispersal in space 1- The Diffusion Model

Population growth rate I is modeled to predict the rate of invasive species population expansion. Maximum dispersal distance (l) and population growth rate (λ) are incorporated into a calculation of population spread rate. The dispersal distances recorded for *M. vimineum* and *A. petiolata* must be converted to D, area colonized per unit of time, before they can be incorporated into the diffusion equation. The maximum dispersal distance affects the rate of population spread, and the high fecundity of invasive plants generates a high probability that at least one seed will establish at the maximum dispersal distance (Okubo and Levin 2001). Population expansion is also influenced by net reproduction I. When no difference is seen among forest management treatments, it is inferred that canopy treatment and past prescribed burning do not affect dispersal distance or seedling establishment. The present study estimates dispersal distances from seedling establishment rather than from seed rain, which is a minimum measure of population growth because it incorporates seed and seedling mortality. The dispersal coefficient is described by the equation:

$$D = \frac{E\left[l^2\right]}{4\tau}$$

in which $E[l^2]$ is the expected dispersal area, and τ is the time interval between generations. Since *M. vimineum* is an annual and reproduces every year, $\tau=1$. Since *A. petiolata* is a biennial and reproduces once every two years, $\tau=2$. *A. petiolata* populations can include both juveniles and reproductive adults and therefore reproduce every year because the non-reproductive, juvenile phase of the biennial habit co-occurs with the reproductive adult phase. However, the expanding edge of the population is represented by individuals that display a biennial habit and therefore disperse seeds every two years. The interior population can serve as a seed source, but the short dispersal distances observed suggests that seed dispersal outside of the existing population comes from individuals on the edge, and so occurs once every two years.

A range of maximum dispersal area was found by looking at the maximum distance of each individual transect. The transect with the shortest recorded maximum dispersal distance represented the lower limit of the maximum dispersal range, and the transect with the longest recorded dispersal distance represented the upper limit. However, this method is susceptible to stochastic variation. Another maximum dispersal distance was found with regression data by calculating the distance at which seedling number=1 on the regression line for each significantly different cohort. This method is less affected by stochasticity but it may underestimate the maximum limit of dispersal distance (which is the most important) because the slope of the regression line is made more negative by the large number of individuals within the the population, and so crosses y=1 before the furthest observed individual.

Seedling establishment data were used to estimate λ for *A. petiolata.* Several study plots contained one isolated reproductive adult in 2010. The number of juveniles present in the vicinity of this reproductive adult was interpreted as per-capita reproduction *r*, which is used to find λ with the equation:

$$\lambda = e^{r}$$

(Silvertown and Charlesworth 2001). *M. vimineum* populations were more dense, and per-capita reproduction was not evident, so values for λ were used from Christen and Matlack (2009) in which *r* was calculated using per-capita seed production.

Dispersal in space 2- *Alliaria petiolata*

A. petiolata was found to have significantly different dispersal distance among treatments, so the range of diffusive spread is reported separately for burn and control sites using both predictors of D (Table 19).

Table 19

Spread rates of A. petiolata

Species	Treatment	*l*	λ	D	C
A. petiolata	Control	0.2-0.7 m (observed)	2-3.6	0.005-0.12 m^2	0.2-0.94 m/ year
A. petiolata	Control	0.29 m (predicted)	2-3.6	0.011 m^2	0.29-0.39 m/ year
A. petiolata	Burn	0.3-0.6 m (observed)	1.6-2.3	0.034-0.045 m^2	0.27-0.64 m/ year
A. petiolata	Burn	0.004 m (predicted)	1.6-2.3	0.000002 m^2	0.0036-0.0043 m/ year

Spread rates of *A. petiolata* I based upon maximum and minimum population growth rate (λ) and dispersal area (D). Observed dispersal ranges were found from observation among replicate transects (*l*) and predicted dispersal was found from finding (y=1) on dispersal regression which expressed stem number (y) as a function of distance.

Spread is sometimes measured as dispersal distance (m) rather than area colonized (m^2) and this spread rate is equivalent to the measures of *l* (Table 15). *A. petiolata* dispersal has been observed at 5.4 m per year (Nuzzo 1999), much greater than the rate observed in the present study. Many of the sites studied by Nuzzo 1999 differed from the present study sites because they were located in a floodplain, and water appeared to be a dispersal vector.

A. petiolata population spread was reduced in plots that had been burned in the past relative to the control. Since the observed dispersal distances were comparable between prescribed burn and control sites, the higher fecundity of control populations appears to have driven the higher rate of spread. No *A. petiolata* populations were identified in harvested sites, but the high light conditions would be expected to produce fecund populations that had high dispersal distances. However, harvested sites would be expected to have dense understory vegetation (as seen in *M. vimineum* and *A. altissima* harvest sites), so the competition may have reduced fecundity.

A. petiolata populations in burned sites covered an area between 20-30 m^2. Based upon distance of spread predicted by a regression line, these sites were colonized 5500-7000 years ago, but this rate is certainly unrealistic because *A. petiolata* was introduced to North America in 1868. The burn sites studied were adjacent to logging and hunting roads, so the population presumably formed sometime after the creation of the roads around 150 years ago (Based upon the establishment of the town of Zaleski). Based upon observed dispersal distances, these sites were colonized 31-111 years ago, which is a more reasonable estimation than the colonization date calculated using predicted spread rates. The populations were not densely populated, and existed as discrete patches separated by several meters of uncolonized area, suggesting that the population contained several satellite populations in the process of coalescing. The satellite populations observed were likely made by long-distance dispersal events, which are not included in the dispersal model and so affect the validity of the estimation of time since colonization. *A. petiolata* control populations varied greatly in area covered. One control covered $<1m^2$ in 2010 and had expanded to about 2 m^2 in 2011. Based upon the observed dispersal rates and the biology of the species (the presence of adult reproductive plants indicates it was present at the site at least one year prior to the study) this area appears to have been colonized 3 years ago. The other *A. petiolata* control population covered a large area around 50 m^2, but the presence of a disjunct sub-population approximately 20 m from the main population influenced the size of this population. It is presumed that the small disjunct population was created by a long-distance dispersal event (which is not addressed in this study) so the uncolonized area between sub-populations is excluded from the population size. The area colonized was closer to 20 m^2, so based upon observed dispersal rates, this population was colonized 21-100 years ago. Based upon predicted dispersal rates, this population was colonized 31-69 years ago. Many of these estimates of colonization time are unrealistic considering *A. petiolata* was first introduced to North America in 1868, which implies that another dispersal mechanism besides gravity, wind, and lodging played a part in the growth of these populations.

Dispersal in Space 3- *Microstegium vimineum*

M. vimineum dispersal did not differ significantly between treatments, so one range of population growth rate is reported for each estimate of D (Table 20)

Table 20

Population spread rates of M. vimineum.

Species	*l*	λ	D	C
M. vimineum	0.3-1.1 m (observed)	1.4-5.3	0.011-0.15 m^2	0.35-2.5 m/year
M. vimineum	0.49 m (predicted)	1.4-5.3	0.03 m^2	0.57-1.1 m/year

Population spread rates of *M. vimineum* (C) based upon population growth rate (λ) and dispersal area (D). Observed dispersal ranges were found from observation among replicate transects (*l*) and predicted dispersal was found from finding (y=1) on dispersal regression which expressed stem number (y) as a function of distance.

The maximum observed value for D was recorded in a plot that had a small gulley running through it, suggesting the presence of a seasonal stream which may have served as a dispersal vector. The present study modeled population expansion at a higher rate than the rate found by Huebner (2010) of 0.16-0.50 m/year. Dispersal distance (*l*) can be reported as a measure of population expansion. Published dispersal distances are comparable to the dispersal distances found in the present study. *M. vimineum* dispersal measured with seed traps in a previous study detected no seed dispersal past 1.5 m (Huebner 2007) and dispersal measured by seedling establishment found no dispersal beyond 1.86 m (Rauschert et al. 2010). Dispersal has been modeled in a previous study using stem lodging as the primary dispersal vector, and so used stem height to find *l*, predicted a linear spread rate of 0.40-0.80 m per year (Miller and Matlack 2010). Much greater dispersal distances have been observed in a previous study along corridors characterized by dispersal vectors such as deer trails (21 m/year), footpaths (3.75 m/year), streams (25 m/year) and sheet flow of water across the forest floor (Miller and Matlack 2010). This implies that natural *M. vimineum* population expansion occurs at a modest rate and a dispersal vector is necessary for the rapid expansion of a population.

M. vimineum spread rate was consistent between treatments, but the area covered by *M. vimineum* populations was much greater in managed forests. *M. vimineum* patches in control forests were found adjacent to hiking trails and covered 10-20 m^2. *M. vimineum* populations in harvests existed throughout the harvested area but were concentrated on skid trails, and existed throughout acres of land. *M. vimineum* populations in burned forests were found exclusively on trails cleared of vegetation, used to stop the spread of fire and used as transport corridors, known as "firelines". These population were only 2 m wide but extended for hundreds of meters along the firelines. The greater area covered by *M. vimineum* populations in managed forests despite the same rate of spread suggests that a dispersal vector existed at one time that facilitated population expansion.

Most *M. vimineum* populations covered large areas that extended along corridors of human movement and consisted of many patches in close proximity, making it hard to estimate the area of one patch. The dispersal mechanism that facilitated the population expansion along miles of road and throughout acres of harvested areas was not the gravity and wind dispersal modeled by the present study, because *M. vimineum* has only been present in North America since 1919 and it would take 200 years to spread just 0.5 km^2. Three populations were isolated from a large, continuous population, and the size of these populations ranged from $<1m^2$-$10m^2$. Based upon observed rates of spread, the population that was $<1m^2$ had been colonized one year ago, and the population 10 m^2 had been colonized 4-29 years ago. Based upon predicted rates of spread, the population $<1m^2$ had been colonized one year ago, and the population $10m^2$ had been colonized 9-18 years ago.

No seedling emergence was observed in *A. altissima* plots, but *A. altissima* has been shown to have low recruitment in closed-canopy forests despite high seed production (Martin and Canham 2010).

Dispersal in space as measured by recording the decline of stem density with distance from the population edge was uniform regardless of canopy treatment for *M.*

vimineum. *M. vimineum* populations expanded uniformly in burn treatments compared to controls, and *A. petiolata* was modeled to expand at a faster rate in control sites than burn sites. Litter removal and soil disturbance are believed to facilitate population expansion following prescribed burn and harvest (Glasgow and Matlack 2007, Oswalt et al. 2007). However, the sites studied had been burned or harvested at least three years before the study, which allowed time for a litter layer to develop and vegetation to colonize disturbed soil. The forests were no longer in the disturbed condition ideal for invasive colonization characterized by bare soil (Glasgow and Matlack 2007, Oswalt et al. 2007) and reduced competition (Meekins and McCarthy 2001, Glasgow and Matlack 2007, Oswalt et al. 2007, de Villalobos et al. 2010). The large populations of *M. vimineum* and other invasives such as *Rosa multifora* and *Lonicera japonica* in harvest sites indicates that population expansion had occurred in these sites because colonization likely began as a single point. *M. vimineum* occurred almost exclusively on skid trails. Since skid trails are usually less than 100 m apart, it was often hard to identify an isolated population edge within the harvested area. In burn sites, *M. vimineum* was found exclusively on firelines in a dense, continuous stand, which indicates that population expansion had already occurred along the fireline. The study populations of *A. petiolata* also occurred near human corridors, but they were not as continuous and dense as *M. vimineum* stands.

Wide distribution of invasive species in managed areas despite limited spread rates can be explained by dispersal that occurs during the management event. One human dispersal event can accelerate population expansion by creating many satellite populations. Although expansion at the population edge is occurring slowly, the creation of many small satellite populations greatly accelerates population expansion by increasing the amount of edge relative to the population area. This happens because population expansion occurs only at the edge of the population, and several small populations have a greater amount of edge per area than one large population. With several satellite populations, the total area colonized is the sum of area colonized at the edge of each satellite population. For a species with a limited dispersal distance, the dispersal at the edge of one large population is limited by the circumference of the population, and most seeds are dispersed within the area already colonized. Satellite populations occupy a smaller area so a greater proportion of seeds are dispersed into uncolonized areas (Moody and Mack 1988). Satellite populations eventually coalesce into one contiguous population. Satellite populations were common throughout the study areas, especially in managed forests. The study sites were often characterized by many discrete colonized areas separated by uncolonized area, like many small populations each expanding from a colonization point. The presence and frequency of satellite populations in managed forests supports the idea that forest management creates long-distance dispersal events that accelerate population expansion by creating satellite populations.

The consistent dispersal distance for *M. vimineum* among treatments is consistent with the idea that the same mechanism is influencing dispersal among treatments. Although *A. petiolata* was seen to have greater rates of population expansion in unmanaged forests, the mechanism driving the observed spread rates were characteristic of a closed-canopy deciduous forest. Gravity, wind, and other natural environmental factors were the only dispersal mechanisms addressed in this study. However, based upon observed natural spread rates alone, *M. vimineum* and *A. petiolata* could not have colonized their current North American ranges during the short time since they were introduced (Nuzzo 1993, Rauschert et al. 2010). Quick range expansion since initial introduction can be explained by long distance dispersal events, which have been found to be the most important factor in spread rate (Coutts et. al 2011). Long-distance dispersal accelerates invasive species spread because it allows population expansion to occur from many points across a large area, and therefore many populations expand to cover a larger area than one expanding population in the same amount of time. Long-distance dispersal is often associated with human activities (Mack 2000). Invasive species are known to be transported by people and invasive distributions are strongly associated with human habitation (Mack 2000). The dispersal model depends upon colonization from a single point, so the disparity between large-scale rate of invasive species spread and small-scale spread rate can be explained by population expansion occurring at more than one point. Points of population expansion are created by long-distance dispersal events that found a disjunct population. The observed distribution of invasive species was probably created by long-distance dispersal facilitating spread rather than population expansion from a single point. The primary dispersal mechanism in the present study sites may have occurred prior to sampling, during the disturbance event. The idea that forest management facilitates seed dispersal is supported by the evidence that invasive populations studied in managed forests existed on heavily trafficked areas such as roads, firelines, and skid trails (pers. observation). Although bare soil existed throughout the burned areas and canopy gaps existed throughout the harvest, invasive species establishment was concentrated on corridors of human travel in the present study sites. Seed dispersal could have taken place during the movement of soil and debris on boots and truck tires. This claim could be tested by surveying invasive populations before a harvest or burn, returning the next year to survey the population distribution, and comparing the observed dispersal rate to a null model based upon natural dispersal rates under similar environmental conditions.

Dispersal in time 1- *Alliaria petiolata* and *Eupatorium rugosum*

The invasive species studied each showed a seasonal pattern of enforced dormancy, consistent with seasonal enforced dormancy found by Sarukhán (1974). Seasonal enforced dormancy indicates that seasonal environmental variation affects the dormancy condition of the seed. The levels of far-red and red light are known to affect seed dormancy (Taiz and Zeiger 2010), and far-red light levels decline after trees produce leaves because leaves absorb red and far-red light (Canham 1985). Cold temperatures are known to initiate enforced dormancy (Taiz and Zeiger 2010). In the spring, warm temperatures and high levels of red and far-red light may promote a state of enforced dormancy in seeds.

Seed survivorship differed significantly among invasive species, and time since burial predicted <1% of the variation in seed mortality in all study species. The variability in mortality rate observed in the present study contrasts the generalization that seed mortality is a linear process, with constant mortality through time (Roberts and Dawkins 1967, Roberts and Feast 1972, Roberts and Feast 1973, Saruhkán 1974). The survivorship curve of each species was compared to a null model of a constant relationship between survivorship and time, with 100% of variability in seed survivorship predicted by time since burial (seed age). A strict relationship between time and seed survivorship shows a constant rate of mortality through time and is described as a type II survivorship curve. A curve showing little variability explained by time may possibly be classified as a type I or type III curve, depending upon whether rate of mortality increased or decreased with time.

A. petiolata survivorship deviated from the null model of a type II survivorship curve because very little variation in seed survivorship (R^2=0.2%) was predicted from time since burial. *A. petiolata* survivorship curve appeared curved rather than straight or stochastic, with risk of mortality increasing with time, suggesting a type I curve. This behavior will lead to the presence of a large, persistent seed bank. Regression on south-facing slopes showed a negative linear relationship between proportion of viable seeds and time but north-facing slopes did not. If *A. petiolata* mortality on south-facing slopes continues at the observed rate the seed bank will be depleted to one seed in 59 years and have a half-life of 9.5 years. However, a type I survivorship curve is characterized by a rate of decline that is not steady throughout time, but increases with time. Rate of decay will likely increase with time and greatly lower the expected lifespan. It appears that at two years, *A. petiolata* has not yet reached the exponential rate of decay characteristic of late-stage type I survivorship curves. The regression also had a very low R^2 value of 0.2, indicating that just 0.2% of *A. petiolata* seed mortality could be explained by time since burial, so the lifespan predicted by a regression on time may be unreliable.

A. petiolata exhibited very low in-field germination. Dormancy can be a desirable trait because seeds are dispersed through time and have the opportunity to germinate during the most favorable season for seedling growth. Dormant seeds can also survive disturbances that will destroy all vegetative plants, which lends resiliency to the population (Stork et al. 2009, Kenneth et al. 2010). However, low germination can have a negative effect on population growth because each year a seed remains dormant, a potential reproductive event is missed. This negative effect is not an issue when seed production is very high (Pickett and McDonnell 1989), which is a trait of *A. petiolata* (Nuzzo 2000). The germination behavior of *A. petiolata* is characteristic of a type IV seed bank as described by Thompson and Grime (1979), with seasonal germination and a large persistent seed bank.

If germination in the field is low enough, populations will contract rather than expand because the number of seedlings produced will be less than the number of adults in the previous generation, so the following generation will have fewer individuals and areas that had previously been populated may contain no individuals. Three transects in the present study showed zero recruitment in the vicinity of a reproductive adult in 2011, indicating low germination or seedling survivorship at these locations. Although the plot at the edge of the study population contained just one or two reproductive adults per m^2 so seed rain was minimal, each adult produced at least 5 siliques with 15-20 seeds each, and seed rain was verified by seeds found in seed traps at 0 m (adjacent to the population). The low recruitment observed is consistent with the results of individual seed bags showing zero seeds germinated in the field after 16 months in the field. After

16 months, each bag recovered showed at least one field-germinated seed. Despite the very low field germination, recovered bags showed very high seed survivorship. This high soil seed survivorship indicates that although *A. petiolata* seeds have not germinated, they may still be present in the soil and germinate at a later date, perhaps when growth conditions are ideal.

No seedlings germinated from *A. petiolata* soil samples, which indicates that either no seeds were present in the samples, or seeds were present but were experiencing dormancy. *A. petiolata* soil samples containing control seeds also showed zero germination. The non-emergence of stratified control seeds suggests that seeds may have been present in the *A. petiolata* soil cores but were experiencing dormancy. Therefore, these data cannot conclude that *A. petiolata* does not form a seed bank.

Assuming the seed bank is part of the population, *A. petiolata* populations will likely be resilient, long-lived, and prepared to rapidly expand following a disturbance. Eradication of an *A. petiolata* invasion would require monitoring sites for removal of individuals for many years to prevent re-establishment from the seed bank.

E. rugosum also shows a soil seed survivorship curve resembling a type I curve, but this species differed from *A. petiolata* in that induced seed dormancy was less common in surviving seeds. This trait may make *E. rugosum* a good competitor when planted in sites invaded by *A petiolata* because the lower proportion of dormant seeds means higher germination can be expected, so dense vegetation will be produced that could compete with *A. petiolata.* Furthermore, the long-lived seeds of *E. rugosum* would make the population's resilience comparable to *A. petiolata.* Rapid, high germination under a broad range of conditions has been shown to be a common characteristic of weedy species seed biology (Baker 1974, Brändle et al. 2003, Pyšek and Richardson 2007). *E. rugosum* showed higher enforced dormancy (germinable seeds) and lower induced dormancy (viable but non-germinable seeds) than *A. petiolata,* indicating that *E. rugosum* seed germination biology is more similar to other invasive species than *A. petiolata.* A negative relationship between *E. rugosum* seed survivorship and time was seen on north and south-facing aspects, but time accounted for <0.5% of variability in survivorship on either slope, which indicates that seasonal or stochastic variation affects *E. rugosum* seed mortality.

E. rugosum is a native herb to North America that is a problematic invasive in East Asia (Yong Ok, et al., 2011, Park, et al. 2011), so the dormancy biology of this species represents the behavior of an invasive species in its natural habitat. *E. rugosum* was seen to have relatively high longevity, but low dormancy. *E. rugosum* is classified as a weedy species and has been reported in 73 counties in the state of Ohio (USDA Plants 2012), while *A. petiolata* has been reported in 37 counties in Ohio (USDA Plants 2012), which suggests that *E. rugosum* shows an invasive habit even in its native range. This says something about the politics of invasion rather than the biology of invasion. *E. rugosum* is more widespread in Ohio than *A. petiolata,* but *E. rugosum* has been a part of the flora for longer than *A. petiolata* and is therefore classified as a “weed” rather than an “alien” or “invasive species”.

Dispersal in Time 2- *Ailanthus altissima* and *Acer saccharum*

Ailanthus altissima resembled a type II survivorship curve because an intermediate number of seeds (~50%) survived for over a year. However, *A. altissima* differed from a type II curve because mortality did not occur steadily through time, but occurred seasonally following the natural germination season of the species. The regression shows that 0.34% (north-facing slopes) and 0.29% of the variation in *A. altissima* seed mortality is explained by a linear relationship to time since seed burial, but in an ideal type II survivorship curve, 100% of variability would be explained by time. The regression predicts that the *A. altissima* seed bank will survive with no further seed inputs for 6.4 years on north-facing slopes and 5.0 years on south-facing slopes and has a half-life of one year on north-facing slopes and 9 months on south-facing slopes. *Ailanthus altissima* was previously predicted to have a low or limited seed bank based upon the species' high germination rates and woody, perennial growth form (Kostel-Hughes et al. 2005).

Soil samples showed zero emergence of seeds from the *A. altissima* soil seed bank. *A. altissima* control seeds planted in forest soil germinated in the greenhouse, which indicates that if seeds had been present in the soil samples, they would not have been dormant. It is inferred that no seeds were present in the *A. altissima* soil samples. These data cannot conclude that *A. altissima* does not form a seed bank because they were unreplicated, and so only positive results would have been meaningful, and would have expressed minimum values for seed bank range and density. Furthermore, it is not uncommon for the species composition of soil seed banks to vary considerably from the species composition of the above-ground vegetation (Thompson and Grime 1979, McDonnell and Pickett 1980) so absence from the soil seed bank does not imply that a species is not an important and long-lasting part of the species pool.

The intermediate level of mortality seen in *A. altissima* varies greatly from the rapid, dramatic mortality observed in the native woody perennial *A. saccharum,* which resembled a type III survivorship curve. However, in a true type III survivorship curve, chance of mortality is very high early in time and decreases as time progresses, so a few individuals survive much longer than the majority. *A. saccharum* differed from a type III survivorship curve because chance of mortality was very high early in time and increased with time until zero individuals survived. Regression analysis predicts that the seed bank will persist for 3.5 months for north and south-facing slopes and has a half-life of one week on north-facing slopes and four days on south-facing slopes. *A. saccharum* showed 100% mortality at 8 months, indicating that this species does not form a persistent seed bank. *A. altissima*, however, showed 54.0% viability at 12 months, which suggests the ability to form a persistent seed bank. This ability is unusual among temperate forest woody perennial species (Pickett and McDonnell 1989, Silvertown and Charlesworth 2001) and may enhance the invasive ability of *A. altissima* by making *A. altissima* more disturbance-tolerant than native competitors. This affects management strategies since controlled sites must be monitored for seedling emergence after vegetative individuals have been eradicated. The high enforced dormancy and low survivorship seen in *A. saccharum* suggests that *A. saccharum* may be an effective competitor in non-disturbed sites where a seedling bank could survive, but *A. saccharum* would be a poor competitor in frequently disturbed sites.

A. altissima experienced enforced dormancy seasonally. High enforced dormancy was seen in spring 2011 and 2012, and almost no germination was seen in the summer and winter months, although at least 50% of the seeds remained viable. These results suggest that *A. altissima* has the ability to form a soil seed bank that germinates seasonally. A seed bank that germinates seasonally promotes invasibility because emergence will occur at the optimal time of year for seedling survivorship and therefore increase recruitment. This trait is unusual in woody species, which usually form a seedling bank of suppressed individuals. This trait makes the species disturbance-tolerant, because viable seeds can survive a disturbance that destroys vegetative individuals. Furthermore, the seeds can remain dormant until a disturbance opens the canopy and creates ideal conditions for growth and establishment. *A. altissima* would be characterized as a type IV seed bank following Thompson and Grime (1979), with seasonal germination and a large, persistent seed bank.

The dormancy behavior of *A. saccharum* was consistent with the biology of a species that forms a seedling bank. A high proportion of seeds experienced enforced dormancy initially, but enforced dormancy decreased with time as the number of viable seeds decreased. After 6 months, zero enforced dormancy was seen and close to zero viability was seen (Zero viability was seen at 8 months). For this species, the next generation is represented by suppressed seedlings “dormant” on the forest floor rather than seeds dormant in the soil. Compared to the seed bank formed by *A. altissima,* the seedling bank formed by *A. saccharum* is less disturbance-tolerant because seedlings are more susceptible to death during a disturbance than dormant seeds. The disturbance-tolerance of seeds compared to vegetation is shown when a disturbance destroys above-ground plants but the disturbed area is recolonized by seeds that survived the disturbance (McDonnell and Pickett 1980, Oswalt et al. 2007, Setterfield et al. 2010). However, the seedling bank of *A. saccharum* is more suited to survival in a closed-canopy forest, and *A. saccharum* has been shown to have dramatically higher seedling recruitment in closed-canopy forest than *A. altissima* (Martin and Canham 2010).

Dispersal in time 3- *Microstegium vimineum*

M. vimineum demonstrated a type III curve in which there was very high mortality early in life and risk of mortality decreases with time. High germination seen in *M. vimineum* study plots and the high enforced dormancy seen during the species' natural germination season suggests that *M vimineum* invests few seeds in a persistent seed bank. The proportion of viable seeds remained steady during times of little germination, and the rise in mortality observed directly following the germination season suggests that in-field germination was a leading cause of mortality in this species, so in-field germination and mortality are the same event. Therefore, the *M. vimineum* seed bank is minimal and most of the population is represented by vegetative individuals after seedling emergence. This affects management because after the above-ground individuals have been eradicated, seedling emergence will be greatly diminished. The upper limit of seed bank survivorship for *M. vimineum* has previously been predicted to be three years (Barden 1987) which is consistent with the survivorship observed in the present study.

Regression did not find a relationship between *M. vimineum* seed survivorship and time on north or south-facing aspects.

Seedlings emerged from a soil seed bank sample taken adjacent to an existing population. This soil sample emergence indicates the presence of seeds <1 m from the population and is consistent with seedling establishment data indicating dispersal occurs >1m from a population edge. It is not surprising that just one replicate contained seeds because forest soil seed banks are known to be heterogeneous on a fine scale (Plue et al. 2010). Also, the enforced dormancy data shows that a high proportion of *M. vimineum* seeds germinate in the first growing season. Since the soil samples were taken after seedling emergence, many of the seeds in the seed bank had already germinated and were exempt from sampling.

The germination behavior of *M. vimineum* was unique among the study species because the majority of seeds germinated in spring of 2011, and very few seeds remained in a state of induced dormancy. During the summer and winter months, the ratio of viable to non-viable seeds remained constant, and almost 100% of viable seeds were in the state of induced dormancy. In the spring of 2012, the ratio of viable to non-viable seeds was still stable, but the viable seeds entered a state of enforced dormancy rather than induced dormancy, so 88% of the viable seeds germinated in the lab. This indicates that *M. vimineum* has the ability to form a small persistent seed bank, but the majority of seeds germinate in the first spring after seed set. This strategy maximizes immediate reproductive return and takes advantage of the exponential nature of plant reproduction. This strategy also minimizes the time a seed spends in the seed bank and therefore minimizes number of seeds that die before they ever germinate. Although only a small proportion of seeds remain dormant to re-establish the population in the event of a population-destroying disturbance, the high per-capita reproductive rate of *M. vimineum* makes just a few seeds capable of quickly restoring a vigorous population. An alternative strategy would be to have a greater number of seeds in a state of induced dormancy. That strategy would provide greater security in the event of a population-destroying disturbance, but the seeds experiencing induced dormancy would miss the opportunity to produce offspring each year they remain dormant, and they would be constantly at risk of being attacked by fungus or granivores. A pulse in seed mortality was seen directly following the in-field germination season of *M. vimineum* in 2011, and the ratio of viable to non-viable seeds remained constant until the spring of 2012, when another rise in mortality occurred following the germination season. This indicates that germination in-field is an important cause of mortality. The in-field germination occurred during the natural emergence season for *M. vimineum.* Therefore, if the seeds in question had germinated in a natural population rather than an experimental seed bag, they would have become members of the population and possibly survived to reproductive maturity. Thus, the high mortality observed in *M. vimineum* seed bags is a reflection of the species' reproductive strategy and not an indication of poor seed survivorship. *M. vimineum* seed bank would be classified as a type III seed bank following Thompson and Grime (1979) in which most germination occurs seasonally but a small persistent seed bank is present.

North-facing slopes were seen to have a lower proportion of viable seeds, which may have been caused by germination that occurred in the field prior to seed bag collection. The higher proportion of seeds in enforced dormancy for *A. altissima* and *M. vimineum* on north-facing slopes and the higher proportion of field-germinated seeds for *A. petiolata* on north-facing slopes support the idea that germination-induced mortality lowered seed survivorship on north-facing slopes among species.

Each species studied showed higher proportions of seeds experiencing enforced dormancy on north-facing slopes than south-facing slopes. North-facing slopes are more cool and mesic than south-facing slopes and they receive sunlight at an indirect angle, which affects the wavelength of light radiated and the length of the photoperiod. Seed survivorship and dormancy can also be related to the lipid contents of the seed, since seeds high in lipids generally have low life expectancy and therefore germinate soon after dispersal (Gardarin et al. 2010). *M. vimineum* showed high enforced dormancy after two months and the lowest life expectancy among the invasive species, so it is possible that *M. vimineum* seeds are under physiological control. Seed survivorship is strongly negatively correlated with seed size (Grime 1981). The largest invasive seeds studied, *A. altissima,* showed intermediate survival and high enforced dormancy during the natural seedling establishment season, and so was inconsistent with the generalization that large seeds have faster mortality rates.

The environment on north-facing slopes appears to promote enforced dormancy of seeds. Therefore, invasions on north-facing slopes may be more resilient to control due to re-emergence from the seed bank. Conversely, the seed bank may not persist as long on north-facing slopes due to elevated losses from germination which is supported by the lower predicted half-life and maximum survival of each invasive on north-facing slopes supports. Harvest or prescribed burn performed on invaded north-facing slopes may experience more dramatic post-management colonization than invaded, managed areas on south-facing slopes.

CONCLUSION

The study species demonstrate various life-history characteristics, which affect invasion. For example, life history affects time between generations. All three species reproduce sexually, but *A. altissima* is dioecious and capable of asexual growth from root sprouts, which allows a damaged adult to quickly grow back, and an isolated individual to propagate asexually when a member of the opposite sex is not present. *M. vimineum* has wind-pollinated flowers while *A. petiolata* and *A. altissima* are insect-pollinated (USDA). Insect pollination influences invasion because more dense populations are needed to facilitate wind pollinations, but insect-directed pollen transfer allows low-density populations to remain reproductive (Silvertown and Charlesworth 2001). Shared characteristics among these three species include high reproductive output, which facilitates invasion by increasing the likelihood that the maximum dispersal distance will be colonized, and a persistent seed bank that promotes invasion by making the species disturbance-tolerant. Therefore, no single plant life history can be classified as "invasive" because invasive species display a variety of plant life histories.

Although long-range dispersal facilitates range expansion (Mack 2000, Coutts 2011) short-range dispersal is responsible for the creation of dense populations that ultimately affect biodiversity and ecosystem processes. Clonal growth as well as gravity, wind, and water dispersal distribute a large number of propagules into a small area, creating a dense population capable of competing with native plants (Meekins and McCarthy 1999; Call and Nilson 2005; Marshall et al. 2009, Flory and Clay 2010). Therefore, dispersal limitation acts as density facilitation, which makes invasive species a threat to forest regeneration. Long-distance dispersal makes invasion a regional phenomenon, but short-distance dispersal makes a species invasive. The study species effectively saturated a small area with propagules. Although low recruitment was observed in *A. petiolata* and *A. altissima* sites, high seed survivorship suggests that dormant seeds are present and may produce a dense population in the future.

Seed dormancy is important to invasion. Seed dormancy allows soil movement to act as a vector for seed dispersal if a dormant seed in the soil behaves as a soil particle. Any event that transports soil, such as sheet water flow (Miller and Matlack 2010), can potentially transport seeds. Seed movement in soil may be responsible for seed movement along graded roads and trails, where human and animal traffic facilitate soil movement (Christen and Matlack 2006). Each of the study species was found to have a persistent seed bank, and so may be transported in soil at any time of the year. Seasonal transitions from induced dormancy to enforced dormancy allow a plant to have some control over germination so seedlings will emerge during the season of highest seedling survivorship (Thompson and Grime 1979). One example of the effect environmental variability has on seed survivorship and dormancy is the difference found between seeds from north and south-facing slopes. Variability seen within-aspect indicates other environmental variables affect seed biology. Although variation existed within species, variation among species was much more consistent and pronounced, which supports the idea that species characteristics are more important than environmental variation in determining seed survivorship and dormancy (Thompson and Grime 1979). In a natural population, input of seeds each year would lead to various seed genotypes stored in the soil seed bank, and so various genotypes may eventually be recruited into the population and recombine in novel ways.

The study species are all perceived as invasive, but contrasts in demography show different ways invasion can be accomplished. An invasive species may achieve dense growth by producing a modest seed bank but high recruitment under a variety of conditions. Conversely, an invasive species may achieve dense growth by showing modest recruitment under closed-canopy conditions, but show high fecundity and high seed survivorship. Therefore, a robust seed bank is present and ready to generate high recruitment under disturbed conditions (Eschtruth and Battles 2009). Regardless of the strategy used to facilitate population expansion or the identity of the species among these three, once a large, dense population has established it will be hard to eradicate because of recolonization from the soil seed bank. Small populations should be targeted before a disturbance allows for rapid population expansion and high recruitment.

A. petiolata, A. altissima, and *M. vimineum* have all been shown to effectively compete with native species (Meekins and McCarthy 1999; Call and Nilson 2005; Marshall et al. 2009, Flory and Clay 2010). This competitive ability not only allows invasive populations to persist, but could prevent regeneration of native species following a disturbance. Since managed forests are, by definition, disturbed, they are susceptible to invasion and therefore arrested succession.

REFERENCES

Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42, 346–353.

Abrams, M.D., 1998. The red maple paradox. Bioscience 48, 355–363.

Abrams, M.D., 2003. Where has all the white oak gone? Bioscience 53, 927– 939.

Aikens, M.L., et al. (2007) The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest. Forest Ecology and Management 252, 144-158.

Albright, T.P. et al. (2010) The ecological niche and reciprocal prediction of the disjunct distribution of an invasive species: the example of *Ailanthus altissima.* Biological Invasions. 12,2413-2427.

Andow, D.A., Kareiva, P.M., Levin, S., and Okubo, A. (1990) Spread of Invading Organisms. Landscape Ecology 4**:** 2/3,177-188.

Baider, C., and Florens, F. (2011) Control of alien weeds averts imminent plant extinction. Biological Invasions. 13:12, 2641-2646.

Baker H.G. (1974) The evolution of weeds. Annual Review of Ecology and Systematics 5, 1–24.

Banks, E.R., and Baker, W.L., (2011) Scale and pattern of Cheatgrass (*Bromus tectorum)* invasion in Rocky Mountain National Park, Natural Areas Journal, 31:4,377-390.

Barden, L. (1987) Invasion of Microstegium vimineum (Poaceae), An Exotic, Annual, Shade-Tolerant, C_4 Grass, into a North Carolina Floodplain. American Midland Naturalist. 118;1.

Bartuszevige, A.M. et al. (2007) Effects of leaf litter on establishment, growth, and survival of invasive plant seedlings in a deciduous forest. American Midland Naturalist 158:2.

Begon, M., Townsend, C., and Harper, J.L. (2006) Ecology: from individuals to ecosystems. Blackwell Publishing, Oxford, UK, Fourth Edition.

Brändle, M., Stadler J., Klotz S and Brandle, R. (2003) Distributional range size of weedy plant species is correlated to germination patterns. Ecology 84, 136–144.

Braun, L., (2001) Deciduous Forests of Eastern North America, The Blackburn Press, Caldwell, NJ.

Brewer, Stephen J. (2011) Per capita community-level effects of an invasive grass, Microstegium vimineum, on vegetation in mesic forests in northern Mississippi (USA). Biological Invasions 13,701-715

Brose, P.H.(2010) Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. Forest ecology and management. 9,1516-1524.

Cain, M.L., Damman, H., and Muir, A. (1998) Seed dispersal and the Holocene migration of woodland herbs. Ecological Monographs. 68:3, 325-347.

Call, L.J., and Nilson, E.T. (2005) Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*) Plant Ecology 176.

Canham, C. (1985) Suppression and release during canopy recruitment in *Acer saccharum.* Bulletin of the Torrey Botanical Club. 112:2, 134-145.

Christen, D. and Matlack, G. (2006) The role of roadsides in plant invasions: a demographic approach. Conservation Biology. 20:2, 385-391.

Claridge, K., and S.B. Franklin. (2002). Compensation and plasticity in an invasive species. Biological Invasions 4,339-347.

Coutts, S. R. et al. (2011) What are the key drivers of spread in invasive plants: dispersal, demography or landscape: and how can we use this knowledge to aid management? Biological invasions. 13,1649-1661.

Doxford, S. W., and Freckleton, R. P. (2012) Changes in the large-scale distribution of plants: extinction, colonization, and the effects of climate. Journal of Ecology. 100,519-529.

Eschtruth, A., and Battles, J. (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. 79:2, 265-280.

Fairbrothers DE, Gray JR (1972) Microstegium vimineum (Trin.) A. Camus (Gramineae) in the United States. Bull Torrey Bot Club 99,97–100

Fotiadis, G., Kryiazopoulos, A. P., and Fraggakis, I. (2011) The behavior of *Ailanthus altissima* weed and its effect on natural ecosystems. Journal of Environmental Biology. 32:6, 801-806.

Flory, S.L., and K. Clay. (2010). Non-native grass invasion suppresses forest succession. Oecologia 164,1029-1038.

Fox, J. (2002) Cox proportional-hazards regression for survival data. Appendix to *An R and S-plus Companion to Applied Regression.*

Gardarin, A. (2010) Seed mortality in the soil is related to seed coat thickness. Seed Science Research.20:4,243-256.

Gavier-Pizarro, G. et al. (2010) Rural housing is related to plant invasions in forests in southern Wisconsin, USA. Landscape Ecology. 25,1505-1518.

Gibson, D.J., Spyreas, G., and Benedict, J. (2002) Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. 129:3,207-219.

Glasgow, L.S., and Matlack, G.R. (2007) Effects of prescribed burning and canopy openness on establishment of two non-native plant species in a deciduous forest, southeast Ohio, USA. Forest Ecology and Management 238.

Gómez-Aparicio, L., and Canham, C.D. (2008) Neighborhood analysis of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. 96, 447-458.

Gorchov, et al. (2011) Treefall gaps required for establishment, but not survival, of invasive Rubus phoenicolasius in deciduous forest, Maryland, USA. Plant Species Biology, 26:3, 221-234

Grime, J.P. (2002) Plant strategies, vegetation processes, and ecosystem properties. 2nd Ed. New York: J. Wiley.

Harper, J.L. (1957) The ecological significance of dormancy and its importance in weed control. Int. Congr. Pl. Prot. 4, 415-20.

Horton, J.L., and H.S. Neufeld. (1998) Photosynthetic responses of *Microstegium vimineum* (Trin.)A. Camus, a shade tolerant, C4 grass, to variable light conditions. Oecologia 114,11-19.

Hu SY (1979) Ailanthus. Arnoldia 39,29–50

Huebner, C.D. (2010) Spread of an invasive grass in closed-canopy deciduous forests across local and regional environmental gradients. Biological Invasions. 12:7, 2081-2089.

Huebner, C.D. (2011) Seed mass, viability, and germination of Japanese stiltgrass (*Microstegium vimineum*) under variable light and moisture conditions. Invasive Plant Science and Management. 4:3, 274-283.

Hyatt, L., Casper, B. (2000) Seed bank formation during early secondary succession in a temperate deciduous forest. Journal of Ecology. 88:3, 516-527.

Iverson, L. et al. (2008) Thinning, fire, and oak regeneration across a heterogeneous landscape in the Eastern U.S.: 7-year results. Forest Ecology and Management 255:7.

Kenneth, S., Setterfield, S., Douglas, M., et al. (2010) Soil seed banks confer resilience to savannah grass-layer plants during seasonal disturbance. Acta-Oecologia International Journal of Ecology, 36:2, 202-210.

Keyser, T.L., Lentile, L.N., Smith, F.W., and Shepperd, W.D. (2008) Changes in forest structure after a large, mixed-severity wildfire in ponderosa pines forests of the Black Hills, South Dakota, USA. Forest Science. 54:3,328-338.

Knapp, L., and Canham, C (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima:* sapling growth and recruitment in canopy gaps. Journal of the torrey botanical society 127:4,307-315.

Kostel-Hughes, F., et al. (2005) Effects of litter depth on the emergence and seedling growth of deciduous forest tree species in relation to size. Journal of the Torrey Botanical Society 132:1.

Lashley, M. et al. (2011) Forage availability for white-tailed deer following silvicultural treatments in hardwood forests. The Journal of Wildlife Management. 75:6, 1467-1476.

Landenberger, R.E., et al. (2007) Seed dispersal of the non-native invasive tree Ailanthus altissima into contrasting environments. Plant Ecology 192:1.

Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82, 227–237.

Mack, R.N. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications. 10:3, 689-710.

Marshall, J.M. et al. (2009) Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods. Journal of the Torrey Botanical Society 136:3.

Martin, P.H., and Canham, C.D. (2010) Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. Oikos 199,807-824.

Martinez-Ghersa et al. (2000) Adaptive traits regulating dormancy and germination of invasive species. Plant Species Biology 15,127-137.

Matlack, G.R., and Schaub, J.R. (2011) Long-term persistence and spatial assortment of nonnative plant species in second-growth forests. Ecography 34,649-658.

Meekins, J.F., and McCarthy, B.C. (1999) Competitive ability of *Alliaria petiolata* (Garlic Mustard, Brassicaceae) an invasive, nonindiginous forest herb. Int. J. Plant Sci. 160 :4.

Meekins, J.F., and McCarthy, B.C. (2001) Effect of environmental variation on the invasive success of a nonindigenous forest herb 11:5.

Miller, N., and Matlack, G. (2010) Population expansion in an invasive grass, Microstegium vimineum: a test of the channeled diffusion model. Diversity and Distributions. 16:5, 816-826.

Mooney, H.A., Hobbs, R.J. (Eds.), 2000. Invasive Species in a Changing World. Island Press, Covelo, CA.

Motsinger, et al. (2010) Effect of midstory and understory removal on the establishment and development of natural and artificial pin oak advance reproduction in bottomland forests. New Forests 39,195-213.

Nuzzo, V.A. (2000) Element stewardship abstract for *Alliaria petiolata* (*Alliaria officinalis*), garlic mustard. Nature Conservancy, Arlington, VA.

Nyland, R.D. (2002) Silviculture: Concepts and Applications. McGraw-Hill 2nd ed.

Nyland, R.D. (2005) Diameter-limit cutting and silviculture: A comparison of long-term yields and values for uneven-aged sugar maple stands. Northern Journal of Applied Forestry. 22:2, 111-116.

Okubo, A., and Levin, S. (1989) A theoretical framework for data-analysis of wind dispersal of seeds and pollen. Ecology. 70:2, 329-338

Okubo, A., and Levin, S. (2001) Diffusion and ecological problems. Springer-Verlag, New York, Ed. 2.

Oswalt, C.M., Oswalt, N.O., and Clatterbuck, W.K. (2007) Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. Forest Ecology and Management 242,727-732.

Plue, et al. (2010) Small-scale seed-bank patterns in a forest soil. Seed Science Research. 20, 13-22.

Pardini, et al. (2009) Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (garlic mustard). Ecological Applications. 19:2, 387-397.

Park, K., et al. (2011) Allelopathic effects of aqueous extracts from Eupatorium rugosum Houtt. And Erigeron annus L. on radicles growth of Lactuca sativa and Raphanus raphanistroides. Allelopathy Journal. 27:1, 65-73.

Pickett, S.T.A., and McDonnell, M.J. (1989) Dynamics in temperate deciduous forest. *Ecology of soil seed banks*. 123-147. Edited by Leck, Parker, and Simpson; Academic Press, Inc.

Prevosto et al. (2011a) Impacts of land abandonment on vegetation: Successional pathways in European habitats. Folia Geobotanica, 46:4, 303-325.

Prevosto et al. (2011b) Can we use shelterwoods in Mediterranean pine forests to promote oak seedling development? Forest Ecology and Management. 262:8, 1426-1433. Jk

Pyšek, P and Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Biological invasions, Ecological Studies 193 (ed. W NENTWIG), 97–126. Springer-Verlag, Berlin & Heidelberg, Germany.

Rejmánek, M., and Richardson, D.M. (1996) What attributes make some plant species more invasive? Ecology 77,1655-1661.

Roberts, H. A. & Dawkins, P. A. (1967). Effect of cultivation on the numbers of viable weed seeds in soil. Weed Research 7, 290-301.

Roberts, H. A. & Feast, P. M. (1972). Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. Weed Research 12,316-324.

Roberts, H. A. & Feast, P. M. (1973). Changes in the numbers of viable weed seeds in soil under different regimes. Weed Research 13,298-303.

Rouget, M., and Richarson, D.M. (2003) Inferring process from pattern of plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. American Naturalist 162:6.

Sarukhán, J., (1974) Studies on plant demography- *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. Journal of Ecology. 52:1,151-177.

Setterfield, S.A. et al. (2010) Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behavior in northern Australian savannahs. Diversity and Distributions 16:5,854-861.

Silvertown, J., and Charlesworth, D. (2001) Introduction to Plant Population Biology.Blackwell Publishing. Ed 4.

Small, C., and McCarthy, B. (2003) Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. Plant Ecology. 164, 37-48.

Stork, N., et al. (2009) Vulnerability and resilience of tropical forest species to land-use change. Conservation Biology. 23: 6, 1438-1447.

Sutherland, S., Hutchinson, T.F.,Windus, J.L., 2003. Understory vegetation. In: Sutherland, E.K., Hutchinson, T.F. (Eds.). Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire. USDA Forest Service General Technical Report NE-299, Northeastern Research Station, Newtown Square, PA, USA. 67–83.

Taiz, L., and Zeiger, E. (2010) Plant Physiology. Sinauer Associates, Incorporated. Ed. 5.

Thompson, K., and Grime, J.P. (1979) Variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology, 67;3,893-921.

Tu, Mandy (2000) Element stewardship abstract for *Microstegium vimineum* Japanese Stiltgrass, Nepalese browntop, Chinese packing grass. Nature Conservancy, Arlington, VA.

USDA (2012) United States Department of Agriculture PLANTS Database. http://plants.usda.gov, 4/16/2012.

Veldman et al. (2009) Selective logging and fires as drivers of alien grass invasion in a Bolivian tropical dry forest. Forest Ecology and Management. 258; 7,1643–1649.

De Villalobos, A.E., Vazquez, D.P., and Martin, J.L. (2010) Soil disturbance, vegetation cover and the establishment of the exotic shrub Pyracantha coccinea in southern France. Biological Invasions. V. 12:5, 1023-1029.

Yong Ok, K., et al. (2011) Comparison of phenolic compounds and the effects of invasive and native species in East Asia: support for the novel weapons hypothesis. Ecological Research. 26:1, 87-94.

APPENDIX

Coordinates of study sites

Site	Region	Species	Treatment	Notes	GPS
Richland Furnace SF	Allegheny Plateau	MV	Shelterwood	Seedbank/dispersal	39˚10.193 N, 82˚36.671 W
Webb Hollow	Allegheny Plateau	MV	Shelterwood	Seedbank/dispersal	39˚18.194N, 82˚24.735W
Zaleski Turkey Mgmt Area	Allegheny Plateau	MV	Burn	Seedbank/dispersal	39˚19’38.66N 82˚18’05.78’’W
Zaleski Turkey Mgmt Area	Allegheny Plateau	AP	Burn	Seedbank/dispersal	39˚20.216 N, 82˚19.010 W
Zaleski Turkey Mgmt Area	Allegheny Plateau	AA	Burn	Seedbank/dispersal	N39˚20.310 W 82˚19.029
Greendale	Allegheny Plateau	MV	Burn	Seedbank/dispersal	39˚25’27.27N 82˚08’56.10W
Greenridge SF 04 shelterwood	Ridge and Valley	MV	Shelterwood	Seedbank/dispersal	39º37’48.77N 78 º29’18.79W
Greenridge SF	R & V	AP	Control	Seedbank/dispersal	39 º38’25.42N 78 º29’32.51W
Manongahela NF	Ridge and Valley	MV	Control	Seedbank/dispersal	Not Available
Sandyridge	Ridge and Valley	MV	Shelterwood	Seedbank/dispersal	39˚04.005 N, 78˚38.730 W
Heavener Mtn	Ridge and valley	MV	Burn	Seedbank/dispersal	38 º37’17.69 N 79 º10’55.79 W
Whetmiller Knob	R & V	MV	Shelterwood	Seedbank/dispersal	38 º40’21.92N 79 º09’02.62 W
Rich Hollow	Allegheny Plateau	AP	Burn	Seedbank/dispersal	39˚ 17 40.83N, 82 21˚ 43.83W
Chestnut Ridge	R & V	MV	Burn	Seedbank/dispersal	Not Available
Little Fork	R & V	AP	Burn	Seedbank/dispersal	Not Available
Little Fork	R & V	MV	Burn	Seedbank/dispersal	Not Available
Middle Mountain	R & V	AA	Burn	Seedbank/dispersal	Not Available
Strouds run SP	Allegheny Plateau	AP,MV,AA	No treatment	Dormancy	39˚ 21 22.57 N, 82˚01 54.13W
Strouds Run SP	Allegheny Plateau	AP,MV,AA	No treatment	Dormancy	39 º20’22.55N 82 º00’56.92W
Zaleski Coal Hollow (South Slope)	Allegheny Plateau	AP,MV,AA	No Treatment	Dormancy	39˚17’38.27N 82˚24’27.62W
Zaleski Webb Hollow (North Slope)	Allegheny Plateau	AP,MV,AA	No treatment	Dormancy	39 º17’38.27N 82 º21’27.62W
The Ridges: OU research	Allegheny Plateau	AP,MV,AA	No treatment	Dormancy	39˚19’27.33N 82˚07’13.43

site					
Wayne NF (glouster)	Allegheny Plateau	AP,MV,AA	No treatment	Dormancy	39˚32.104 N, 82˚05.376 W
Zaleski State Forest	Allegheny Plateau	MV	control	Seedbank/dispersal	39˚16’50.51N 82˚21’43.72W
Zaleski State Forest	Allegheny Plateau	MV	control	Seedbank/dispersal	39˚16’54.91N 82˚21’38.04W
The Ridges OU research site	Allegheny Plateau	AP	Control	Seedbank/dispersal	39˚19.455 N, 82˚07.211 W
Strouds Run SP	Allegheny Plateau	AP	Control	Seedbank/dispersal	39˚20.614 N, 82˚00.911 W.
Clary Site (2)	Allegheny Plateau	AA	DLC	Seedbank/dispersal	(39˚10.995N, 82˚48.113 W) (39˚10.837 N, 82˚47.964 W)
Clary Site	Allegheny Plateau	MV	DLC	Seedbank/dispersal	39˚10.842N, 82˚47.964 W

AA=*A. altissima,* AP=*A. petiolata,* MV=*M. vimineum*