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ORIGINAL PAPER

Spread of an invasive grass in closed-canopy deciduous forests across local and regional environmental gradients

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Abstract Spread of *Microstegium vimineum*, an invasive exotic grass, in closed-canopy forests of West Virginia, U.S. was evaluated across a local (roadside to forest interior) and regional (across two geographic provinces) environmental gradient. Seed dispersal distances from roadside populations into forest interiors based on seed rain and soil seed bank data were determined. Colonization and extinction of *M. vimineum* patches were followed over three years (2005–2007), and spread rate was estimated using a reaction-diffusion model. Direct seed dispersal from the roadside populations occurred primarily adjacent to the maternal plants, indicating that the disjunct *M. vimineum* patches within the forest interiors occurred via secondary seed dispersal over longer distances. Patches of *M. vimineum* were found as far as 45 m into the forest interior, but *M. vimineum* seed in the seed bank were only found within 10 m of the roadside population. Colonization rates of the forest interiors were significantly higher for the more mesic sites than the more xeric sites. The same trend was noted for the spread rate. Radial spread rates ranged between 0.16 and 0.50 m year^{-1} and forest interiors were estimated to become saturated with *M. vimineum* in anywhere between 10 (more mesic sites) and 59 (more xeric sites) years. These results support the possibility of accelerating spread rates in forest interiors caused by more long-distance dispersal events, but slowed by a reduction in *M. vimineum* fitness in shaded or relatively dry environments.

Keywords Environmental gradient · Forest interiors · Invasive plants · *Microstegium vimineum* · Seed dispersal · Spread

Abbreviations

ITIS	Integrated Taxonomic Information System
MNF	Monongahela National Forest
PAR	Photosynthetically active radiation
R–V	Ridge and Valley Province

Introduction

Closed-canopy forests are susceptible to establishment of shade-tolerant, invasive plants (Martin et al. 2009; Huebner 2009, this issue), but may be less susceptible to rapid spread of these invaders compared to open environments (Rejmánek and Richardson 1996) and corridors, such as roadsides (Christen and Matlack 2006). Site vulnerability to rapid spread may decrease under relatively stressful or less than optimal environmental conditions (Gilbert and Lechowicz 2005; MacDougall et al. 2006). Spread of invasive plant species is driven by effective long- and short-distance

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dispersal as well as site suitability (Theoharides and Dukes 2007). Examples of short-distance dispersal include corridor and leading-edge dispersal, both of which usually involve continuous frequency of dispersal with few to many propagules. 'Sweepstakes' long-distance dispersal occurs when propagules move well beyond the dispersal range of the original population, i.e., via bird dispersal, such that the original source population is difficult to identify. 'Jump' long-distance dispersal occurs when new populations are found at a distance and are physically disconnected, but originate from an identifiable seed source, such as a roadside patch. Both 'sweepstakes' and 'jump' dispersal occur infrequently with few propagules (Wilson et al. 2009). Understanding the relative importance of short- vs. long-distance dispersal of invasive plant species into forests and how they may vary under different environmental conditions may improve our ability to predict spread rates.

Microstegium vimineum (Japanese stiltgrass) is a shade-tolerant, annual grass invading Eastern and Midwestern forests of the U.S. Its growth is most productive under mesic conditions, making it somewhat drought intolerant (Barden 1987; Redman 1995; Webster et al. 2008). Likewise, despite being shade-tolerant (Winter et al. 1982; Horton and Neufeld 1998), *M. vimineum* manifests a significant reduction in growth and reproduction under photosynthetically active radiation (PAR) values less than 5–18% of full sunlight (Claridge and Franklin 2002; Cole and Weltzin 2004, 2005; Cheplick 2005). While *M. vimineum* does occur in closed canopy forests which typically have PAR values below 5% (Cole and Weltzin 2004; Huebner 2009, this issue), the smaller plant size and lower seed production of *M. vimineum* associated with closed-canopy forests, compared to roadside environments, could result in local extinctions within these high-shade environments similar to what is found with Allee effects (Groom 1998; Courchamp et al. 1999). It is currently unknown if conditions found in forest interiors limit *M. vimineum*'s spread into closed canopy forests from roadsides (local gradient with possible light limitations) or if spread rate will vary across a regional environmental gradient (possible moisture limitations).

This observational study addresses the following question: How far are *M. vimineum* seed dispersed from roadside populations into adjacent closed-canopy forests and what is the spread rate of *M. vimineum* in closed canopy forests across a local (roadside to forest interior) and regional (two geographic provinces) environmental gradient?

Methods

Study species and study area

Microstegium vimineum (Trin.) A. Camus (Integrated Taxonomic Information System (IT IS); Gleason and Cronquist 1993) is an Asiatic grass that was accidentally introduced to the U.S. (Knoxville, Tennessee) in 1919 (Fairbrothers and Gray 1972) and first documented in West Virginia in 1956 (Huebner 2003). Sixteen sites in West Virginia that all had contiguous roadside populations of *M. vimineum* adjacent to undisturbed, closed-canopy, deciduous forests were selected. These sites were located over three general regions: (1) five in the Fernow Experimental Forest, Cheat-Potomac Ranger District of the Monongahela National Forest (MNF) in the Allegheny Plateau (Fernow), (2) six in Cooper's Rock State Forest also in the Allegheny Plateau (Cooper), and (3) five in the Seneca Rocks area of the Cheat-Potomac Range District of the MNF in the Ridge and Valley Province (R–V; see Huebner 2009, this issue for a diagram of site locations). Annual precipitation averages approximately 160 cm for both the Fernow and Cooper sites, while it is about 79 cm annually for the R–V sites (Clarkson 1964). The highest average annual temperature is approximately 23–25°C for the Fernow and Cooper sites, but 30°C for the R–V sites (NOAA, National Climatic Data Center website). Additional details about the sites and this species are in Huebner (2009, this issue).

Sampling design

Each site was composed of a 10 m transect located parallel to a contiguous roadside *M. vimineum* population that was at least 20 m long. From this roadside transect, nine perpendicular transects, each 1.25 m apart and 50 m long radiated into the adjacent forest. The two edge transects and a central transect 5 m from either edge (the systematic transects) were used to systematically place 1-m^2 plots (actual area of 1.2 m^2, Huebner 2009, this issue) at the roadside just outside the forest canopy edge with subsequent 1-m^2 plots located in the forest interior every 5 m until 20 m, and then every 10 m until 50 m. Two transects were located halfway between the edge transects and the central transect and were used to estimate the leading edge of the invasion front (hereafter called the front transects). Starting at 0 m (forest edge) on the front transects, contiguous 1-m^2 plots were placed only if *M. vimineum* was present. The remaining three transects were used to help locate new 1-m^2 *M. vimineum* patches to avoid potential overlap (Fig. 1).

Local gradient

Actual seed dispersal from the roadside *M. vimineum* populations into the forest interior was determined using the six sites at Cooper, because these could be visited every 2 weeks. A 10 cm × 26 cm sticky trap was placed flat just behind (closer to the 50 m end of the three main transects) each 1-m^2 plot along the three systematic transects using four nails (Fig. 1). Traps were placed in these positions whether or not any *M. vimineum* was in the adjacent plot; there was no *M. vimineum* for at least 100 m beyond the 50 m transects at any of the sites. The traps were established September 13, 2005 and changed every 2 weeks until October 31, 2005 (when plants senesced). *Microstegium vimineum* seed found on each trap were summed for the entire time period at each distance for each site.

Just outside each of the systematically located 1-m^2 plots a 15 × 15 cm and 10 cm deep soil sample was taken in late August for a seed bank analysis. The seed bank analysis focused on whether or not *M. vimineum* germinated and not other germinating plant species. Evaluation of the seed bank was conducted using two walk-in growth chambers at a constant light intensity of 1500 μmol m^{-2} s^{-1} with ample water, placing the collected soil on a 2-cm deep bed of Redi-Earth potting soil. The information on the actual seed dispersal and the seed bank was also used to parameterize a model estimating spread rate.

Actual seed dispersal and seed bank data (both collected in 2005 only) were evaluated using seed counts of each over the 0–50 m distances (combining transect values at each distance). Site differences for distances, sites, and interactions between site and distance in seed bank formation were determined using a generalized linear model and a gamma distribution (best fit for the skewed distribution) with a log link function (nonlinear transformation of the predicted values; Proc GenMod, SAS v. 9.1).

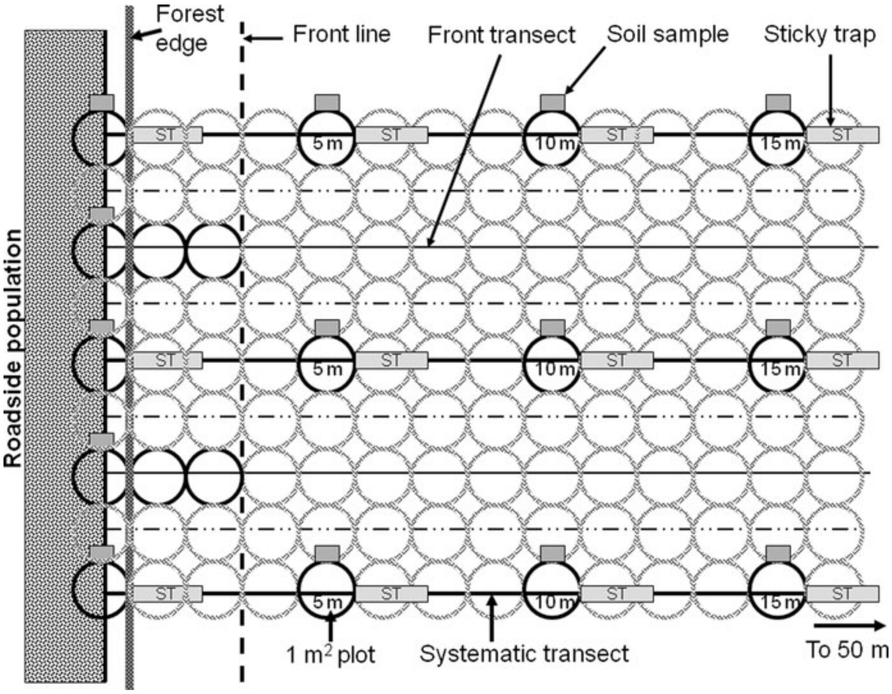


Fig. 1 Sampling design. Only 1-m^2 plots through 16 m for each 50 m transect are shown. *Darker circles* are systematically sampled plots or examples of known contiguous plots within an example front line distance (which differed with site). *Lighter circles* between the roadside and front contain *M. vimineum*, while *lighter and darker circles* beyond the front line *potentially* contain *M. vimineum*

Regional gradient

The invasion front for each site was determined by measuring the longest colonized distance along two central transects at which *M. vimineum* patches were no longer contiguous (using a 1-m^2 resolution) from the roadside into the forest interior. Patches (1 m^2 or less in size) of *M. vimineum* were counted within the 10 m × 50 m area in the 369 (41 × 9) circular 1-m^2 possible patches that could be colonized (and potentially documented in a future measurement) by *M. vimineum* (Fig. 1). Number of new patches and extinct patches per site and year were tallied.

In order to compare *M. vimineum* population growth among sites, the net reproductive rate (R_0, which also equals the annual rate of increase (λ) for annual plants), was estimated between 2005–2006 and between 2006–2007 using $R_0 = N_{t+1}/N_t$ (where $N =$ number of colonized patches and $t =$ years). The instantaneous rate of increase (r) was estimated using $r \sim\ = \ln(\lambda)$ or in this case $\ln(R_0)$. The time to complete forest understory saturation ($N_t = 369$ patches) was calculated using $N_t = N_0 e^{rt}$ (Silvertown 1990). The 369 patches were used as the saturation point because doing so allows for easier future comparisons of actual population growth with predicted growth. Use of $N_t = N_0 e^{rt}$ assumes exponential population growth and that *M. vimineum* is not density-dependent. Given the small stem counts compared to those at the roadside (10 vs. 1000 s per 1-m^2), this assumption is considered legitimate, at least for early establishing forest interior populations.

Rate of spread (V) was estimated using $V = 2(rD)^{0.5}$, a modified Fisher (1937) reaction-diffusion model, where $D =$ the diffusion coefficient or $D = (4\ \mathrm{M}^2)/\pi$, where $M =$ mean radial distance (m) of second-generation progeny from the parent plants (Skellam 1951; Allen et al. 1991). M was estimated using average plant height for interior *M. vimineum* plants for each site type (Huebner 2009, this issue). Use of the simple diffusion equation to estimate spread rate assumes exponential growth, relatively constant site conditions, and radial short-distance dispersal (Shigesada et al. 1995).

Differences in invasion-front distance, colonization, extinction, spread rate, and time to forest understory saturation between sites were evaluated using a generalized linear model with a gamma response distribution and log identity link function (Proc GenMod, SAS v. 9.1). Individual years for the front-line distance variable and paired years (2005–2006, 2006–2007) for the remaining variables were assessed separately for two reasons: (1) sample size changed as new plots were colonized by *M. vimineum*, meaning the analyses may not be truly a repeated measure (nor are they completely unbiased), and (2) the sample size did not allow for an additional covariate of time.

Results

Local gradient

No *M. vimineum* seed was found on the sticky traps beyond 0 m on any of the 18 (three per six sites) transects in the Cooper sites. The sticky traps at 0 m captured between 0 and 324 seed during the 49 days of collection or an average of 77.61 seed per site. Most of the seed fell during the second 14-day collection period (starting Oct. 11, 2005). *Microstegium vimineum* germinants from the seed bank occurred at 0, 5, and 10 m with no germinants found beyond 10 m and most being found at 0 m. Seed found at 5 and 10 m were only associated with the R–V sites. The *M. vimineum* seed bank was marginally significantly different among the sites ($P = 0.059$). The R–V sites had the most germinants with 9,688 m^{-2} per site at a 10 cm depth, followed by Cooper with 5,990 m^{-2} per site, and the Fernow with 1,563 m^{-2} per site. At the 0-m distance, 8,750, 5,890, and 1,406 germinants m^{-2} per site occurred at R–V, Cooper, and Fernow, respectively. The seed bank did differ significantly among the distances ($\chi^2 = 11.43$, $P = 0.0033$), with estimable differences only possible for 0, 5, and 10 m because no seed was found at the other distances. The 0-m distance was significantly different from 5 m ($\chi^2 = 8.00$, $P = 0.0047$) and 10 m ($\chi^2 = 9.80$, $P = 0.0017$), but 5 and 10 m did not differ significantly from each other ($P = 0.53$), having on average 244 and 98 germinants m^{-2}, respectively. There was no significant interaction between site and distance ($P = 0.14$).

Regional gradient

The spread rate of *M. vimineum* at these sites ranged between 0.16 and 0.50 m year^{-1}. There was no significant difference in population size, number of extinctions, the estimated invasion front, the distance of the farthest patch from the roadside, time to saturation, or the spread rate among sites in any year. However, both the Fernow and Cooper sites had significantly more colonizations than the R–V sites, but only in 2006 ($\chi^2 = 8.27$, $P = 0.016$), the driest year (Huebner 2009, this issue). Based on the means, there was a trend for the invasion fronts in the R–V sites to be extended further into the forest (3–8 m) but to exhibit slower spread rates (0.16–0.19 m year^{-1}) as well as a longer time-to-understory saturation (51–58 year) compared with both the Fernow and Cooper sites (Table 1). This suggests that the seed source of *M. vimineum* at the R–V sites may be from populations along the invasion front (i.e., diffusive spread) while the spread of the Fernow and, to a lesser extent, the Cooper populations tends to be facilitated by the formation of spatially-disjunct patches in the forest interior instead of the invasion front. The individual patches of *M. vimineum* in the forest interior remained composed of very few stems per patch for the three-year period (Huebner 2009, this issue), which supports the assumption of no negative density-dependent effects during this time period.

Distance distribution histograms of *M. vimineum* for the forest interior (plots 5 m and beyond, Huebner 2009, this issue) reveal a leptokurtic distribution (Fig. 2a–d). Differences among sites suggest significant regional site-type heterogeneity. The Cooper and Fernow site type distributions differed from the R–V distribution by having longer and fatter tails, suggesting more long-distance dispersal (based on colonization rather than actual seed dispersal) at these sites. The R–V site type distribution had the shortest tail, suggesting more diffusive spread and limited long-distance dispersal.

Discussion

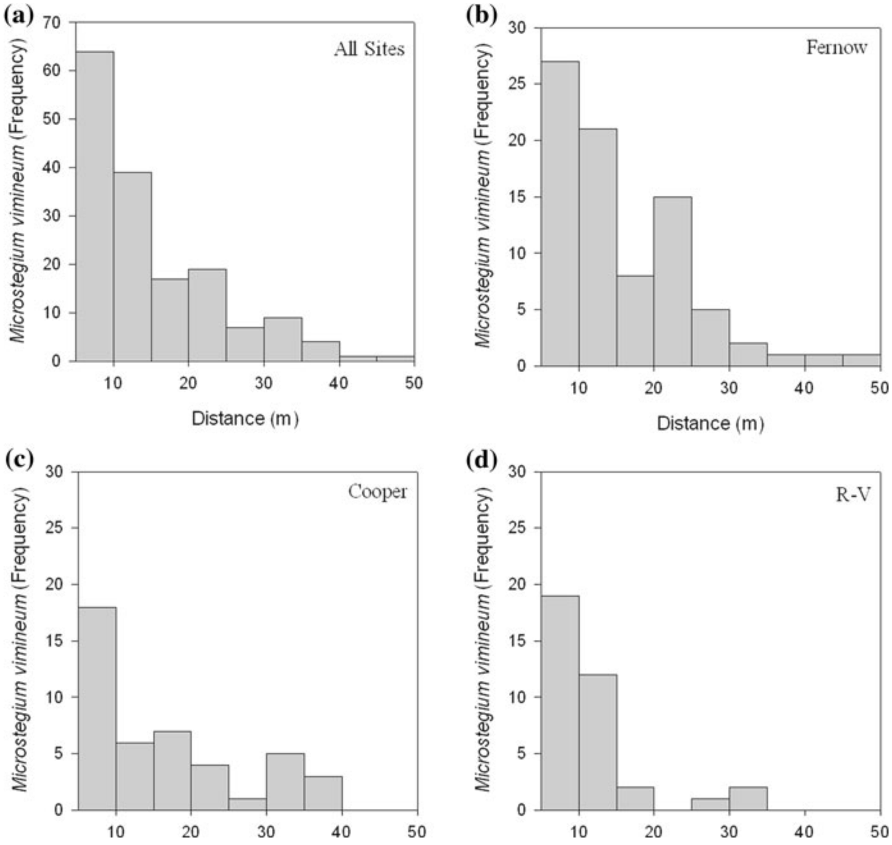
Most *M. vimineum* seed fell with the maternal plants, yet small disjunct patches, often of only a single stem, commonly occurred in the forest interiors, suggesting that dispersal occurred through vectors other than wind, such as soil, water, and animals (i.e., deer, rodents, or humans). All of these vectors, except possibly flooding, may explain the rather haphazard but more rapid establishment of individual *M. vimineum* patches in the forest interior, unlike what was seen with the slower encroaching invasion fronts. Some of these disjunct patches were found as far as 45 m, with 27 m being the average farthest distance. These findings agree with

Table 1 Mean *Microstegium vimineum* population growth data for each site type and year based on all plots containing *M. vimineum*[a]

Variable	Year	Regional Gradient (most mesic to most xeric site types)		
		$N = 5$ Fernow	$N = 6$ Cooper	$N = 5$ R–V
Population size (# 1-m^2 plots)	2005	29.40 (4.12)	31.0 0(1.65)	52.00 (11.70)
	2006	44.40 (7.16)	45.50 (5.80)	62.20 (15.57)
	2007	52.20 (6.96)	48.50 (5.35)	65.40 (14.78)
Colonizations (# 1-m^2 plots)	2006	10.00 (2.16)a	5.50 (2.75)a	1.40 (0.68)b
	2007	9.60 (3.41)	4.67 (1.87)	3.40 (0.81)
Extinctions (# 1-m^2 plots)	2006	1.00 (0.77)	1.00 (0.49)	1.80 (0.49)
	2007	3.60 (1.08)	2.33 (1.31)	2.20 (0.73)
Front (m)	2005	3.50 (0.47)	3.75 (0.78)	6.25 (1.31)
	2006	4.25 (0.93)	5.00 (1.80)	7.75 (1.74)
	2007	4.50 (0.85)	5.00 (1.80)	8.25 (1.70)
Farthest patch (m)	2005	8.44 (3.79)	10.8 (4.61)	18.26 (3.33)
	2006	21.88 (2.49)	20.94 (7.63)	15.14 (5.46)
	2007	27.08 (6.96)	17.68 (7.47)	15.91 (5.06)
Time to saturation (years)	2006	10.35 (5.14)	21.13 (11.22)	58.31 (35.70)
	2007	14.38 (6.17)	40.25 (19.13)	51.75 (22.81)
Spread rate (m year^{-1})	2006	0.50 (0.08)	0.44 (0.10)	0.16 (0.14)
	2007	0.30 (0.10)	0.16 (0.07)	0.19 (0.08)

[a] Comparisons were analyzed using a generalized linear model. Sites with different letters were significantly different ($P < 0.05$). If no letters are shown, there was no significant difference

Fig. 2 **a–d** Colonization distribution for *M. vimineum* frequency (out of 171, 83, 47, and 41 plots in all sites (**a**), the Fernow sites (**b**), the Cooper sites (**c**), and the R–V sites (**d**), respectively) by site for 2007 starting at 5 m. Year 2005 and 2006 showed similar distributions



Neubert and Caswell's (2000) assertion that long-distance (likely 'jump' dispersal (Wilson et al. 2009)), even if rare for *M. vimineum* compared to the amount of seed dropped adjacent to the maternal plants, will determine *M. vimineum*'s rate of spread. Based on height data alone, the invasion front is moving toward the forest interior at a linear rate of approximately 0.50–0.70 m year^{-1}. As canopy cover increases along the roadside-to-forest gradient, with much of the increase in cover occurring at 5 m and beyond, the linear spread rate along the invasion front decreases, ranging between 0.0004 and 0.048 m year^{-1}, as the plants become shorter. This estimated linear spread rate is much less than the radial rate calculated using $V = 2(rD)^{0.5}$, which ranged between 0.16 and 0.50 m year^{-1}. Both the linear and radial spread rates of *M. vimineum* are less than most spread rates estimated for native forest understory species migrating from an old-growth forest into an adjacent successional forest, which range from 0.04 to 2.50 m year^{-1} (Matlack 1994), but are not unusual for grasses (Cheplick 1998). *Microstegium vimineum*'s rate of spread appears to be much slower than that estimated for *Mimosa pigra* L. (giant mimosa; ITIS) in Australia, which showed spread rates of 18.3 and 76 m year^{-1}, based on seed traps and aerial photographs, respectively (Lonsdale 1993). The spread rates of *M. vimineum* were not measured across a landscape, though such coarse-scale spread rates are also needed, but were limited to a homogeneous forested area. Frappier et al. (2003) used a reaction-diffusion model to estimate *Frangula alnus*' P. Mill. (glossy buckthorn; ITIS) rate of spread within a single stand as 6.3 m year^{-1}. This estimate is, not surprisingly, greater than that of *M. vimineum*'s, because *F. alnus* is a much larger plant, reaching 7 m in height (Gleason and Cronquist 1993), and its seed are bird-dispersed (Frappier et al. 2003). Thus, it appears that many native forest species (and some nonnative plants) should have a dispersal-rate advantage over *M. vimineum* in terms of spread within forest interiors, given equally abundant seed sources. However, where roadsides are dominated by *M. vimineum*, the abundance of available *M. vimineum* seed increases its likelihood of dispersal, establishment, and spread.

The more rapid, patchy movement of *M. vimineum* seed into the forest interior did not result in a detectable forest interior seed bank in 2005. While a subsequent seed bank sample now may reveal more *M. vimineum* seed beyond 10 m (especially in the R–V sites), these results suggest that detection of such seed is still likely to be nominal unless the samples are taken adjacent to existing patches of *M. vimineum*. Nonetheless, an encroaching invasion front, though slower in spread, will be a greater source of seed-bank germinants than the disjunct patches further in the forest interior until coalescence of the patches begins to occur. Roadside populations of *M. vimineum*, thus, not only encompass the majority of the available above-ground propagules, but they also will be the source of most of the available seed bank.

On average (all sites and years together), *M. vimineum* was spreading at a rate of 0.29 m year^{-1} and the time to understory saturation of these relatively homogeneous sites was 32.70 years. While not significant, the spread rate and time to saturation for the R–V more xeric site type did manifest a trend of being slower and taking longer, respectively. There were also significantly fewer colonizations during this 3-year period at the R–V sites in 2006. The fact that the R–V sites have been invaded longer than the Cooper and Fernow sites (Huebner 2009, this issue) is a confounding factor that may explain the wider invasion front and consequently fewer available patches to colonize overall, which in turn may overestimate the spread rate into the remaining R–V patches. The significant lack of new colonizations beyond the invasion front in the R–V sites shows that *M. vimineum* in the more xeric site type is more dependent on its invasion front for any kind of spread during this period. What appears to be relatively random establishment of disjunct patches in the forest interior is less likely to occur in more xeric sites.

One can predict that existing and new disjunct patches will increase in number, grow in size, and eventually coalesce, leading to an accelerated spread rate over time at all site types (Shigesada et al. 1995). However, patch growth and coalescence under low-light conditions for *M. vimineum* (where stems are short and fewer in number and produce less seed) will be relatively slow, making the number of new patches each year (instead of their individual growth in size) the predicted driving force behind *M. vimineum*'s rate of spread in forests. Moreover, the likelihood of an Allee effect increases if seed dispersal from adjacent high-light environments (i.e., roadsides) is nominal and a stochastic environment (i.e., fluctuating drought conditions) exists (Saether and Engen 2004).

There are management protocols that argue for the removal of disjunct (satellite) populations of an invading species (Moody and Mack 1988; Sharov and Liebhold 1998; DiTomaso 2000; Masters and Sheley 2001; Taylor and Hastings 2004) before they have a chance to grow and coalesce, prior to focusing on the larger core populations and their seed sources (e.g., the *M. vimineum*'s roadside populations). In contrast, according to Hulme (2003), core populations contribute proportionally more to a population's growth through long-distance dispersal, suggesting that successful control and eradication are more likely if the focus is on the core population. I argue further that the radial rate of spread from the roadside seed source (around 0.4 m year^{-1} for the more mesic sites and 0.18 m year^{-1} for the more xeric sites) vs. the rate of linear spread of a given satellite patch (less than 0.0015 m year^{-1}), makes treating the roadsides a more effective approach for *M. vimineum*. Indeed, if the roadside seed source is removed, it is possible that many of the small patches found in the forest interior may go extinct without any proactive treatment due to stochasticity or possible Allee effects (Lewis and Kareiva 1993; Taylor and Hastings 2005). Many of these *M. vimineum* patches may produce so few seed that success of simply reproducing oneself, much less growing in population size, is unlikely, especially in sites with relatively high environmental stochasticity (Lande 1998) such as the more xeric sites in this study. However, budget constraints often prevent focusing on core populations. Instead, it may be necessary to focus on the secondary long-distance dispersal vectors. For instance, removal of deer (Eschtruth and Battles 2008) and humans as dispersal vectors using fencing or other similar barriers could reduce *M. vimineum*'s rate of spread into forests.

The spread estimates of this research are based on Fisher's equation (Fisher 1937), which assumes diffusive movement of individuals or a normal distribution of dispersal distances. The Fisher model also assumes that the seed of all individuals have the same propensity for dispersal (Neubert and Parker 2004). This research does confirm a leptokurtic distribution of colonization distances within the forest understory for *M. vimineum*, and the curve shape varies with site type, suggesting spatial stochasticity is important. Consequently, integrodifference equation models (Kot et al. 1996) or similar more complex models may be more appropriate than the Fisher's equation to estimate landscape-scale spread rates for *M. vimineum*. The spread rate estimates, especially for the Cooper and Fernow sites are likely underestimated because long-distance dispersal is more evident in these areas. It is beyond the scope of this paper to develop the appropriate integrodifference equations to estimate *M. vimineum*'s spread. Nonetheless, these results do provide the support for future models to factor in the different dispersal kernels defined by local and regional gradients, the temporal stochasticity most evident in the growth and reproductive data, and the possibility of an Allee effect (Latore et al. 1998; Clark et al. 2001; Kot et al. 1996; Kot et al. 2004; Neubert and Parker 2004).

Strategic management of *M. vimineum* may be best accomplished by removing the predominant roadside population source of propagules instead of slowing the spread by focusing on the satellite populations beginning to colonize the forest interiors. This strategy of focusing on the core populations will be most effective under more mesic conditions, where long-distance establishment of disjunct forest interior populations is more likely.

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