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Strategic management of five deciduous forest invaders using *Microstegium vimineum* as a model species

Cynthia D. Huebner
USDA Forest Service, Northern Research Station

Abstract. This paper links key plant invasive traits with key landscape traits to define strategic management for five common forest invaders, using empirical data of *Microstegium vimineum* dispersal into forests as a preliminary model. *Microstegium vimineum* exhibits an Allee effect that may allow management to focus on treating its source corridor populations at local scales. Forest interior populations without a constant seed source from the corridor populations could potentially go extinct on their own. In contrast, species with long-distance dispersal are likely best managed at a landscape scale, focusing on new establishment sites rather than on removal of source corridor populations.

Introduction

Effective management of invasive species in forests requires the ability to predict their establishment and spread. While there are several studies evaluating the characteristics of both invasive species (Rejmanek and Richardson 1996, Reichard and Hamilton 1997, Kolar and Lodge 2001) and landscapes vulnerable to invasion (Burke and Grime 1996, Higgins et al. 1999, Huebner and Tobin 2006), literature evaluating the effects of landscape spatial patterns on the invasion process is relatively depauperate (Higgens and Richardson 1996, With 2002). Linking spatial patterns of disturbance, resource availability, and vegetation types with demographic and biological processes of establishment and spread should result in a more strategic approach to management (Figure 1).

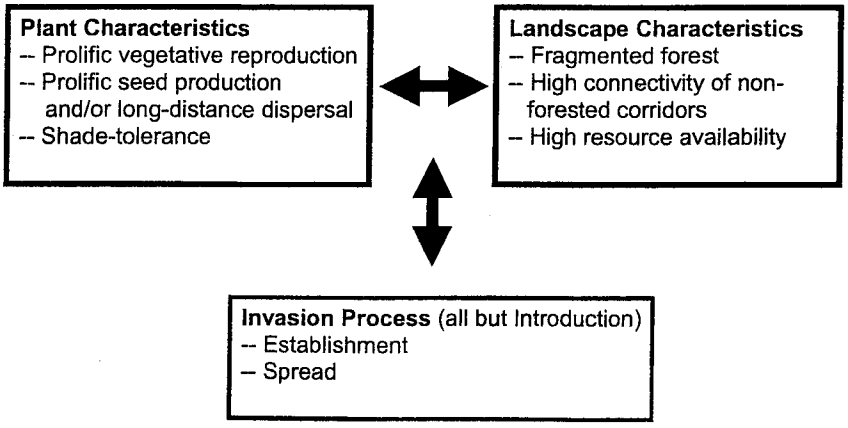


Figure 1. Linking key plant invasive characteristics with key landscape characteristics to predict spread of an invasive plant.

The ability to reproduce prolifically over long distances by seed (Cain et al. 2000, Wang and Smith 2002, Nathan 2006) and vegetatively (Kolar and Lodge 2001) under both high and low light conditions have been documented as traits shared by many known invasive plants. Likewise, several studies attribute relatively high resource availability (which may change with disturbance; Huenneke et al. 1990, Bergelson et al. 1993), fragmentation, and increased connectivity of non-forest corridors (Parendes and Jones 2000) as landscape attributes that promote invasion.

The objectives of this paper are to (1) predict establishment and spread of *Microstegium vimineum* (Japanese stiltgrass) using empirical data linking plant demography and biology with landscape characteristics, and (2) hypothesize how *Alliaria petiolata* (garlic mustard), *Ailanthus altissima* (tree of heaven), *Rhamnus cathartica* (common buckthorn), and *Celastrus orbiculatus* (oriental bittersweet) would differ from *M. vimineum* spread.

Methods and Materials

The Species. Table 1 summarizes the five species based on three key invasive traits – shade-tolerance, long-distance seed dispersal, and clonal growth. *Microstegium vimineum* is shade-tolerant (Winter et al. 1982) and reproduces by seed (Gleason and Cronquist 1993). It may spread vegetatively by rooting at the nodes (Hoshikawa 1969) but is not clonal. Both cleistogamous (closed) and chasmogamous (open) flowers are produced (Tanaka 1975), though the chasmogamous flowers tend to be associated with populations located in high light (Barden 1987). The lack of chasmogamous flowers in shaded plants may place such populations at a disadvantage in terms of lower flower and seed production (due to smaller plants), and seed dispersal over much shorter distances (seeds remain on the plant until plant senescence). Seeds of *M. vimineum* are thought to be dispersed by water and animals (Mehrhoff 2000). Wind dispersal is possible but has not been confirmed. Some research suggests that short-lived grasses, such as *M. vimineum* would favor short distance dispersal because the risk of finding a non-safe site for germination is too great (Collins and Uno 1985). *Alliaria petiolata* is similar to *M. vimineum* in that it is shade-tolerant (Byers and Quinn 1998, Welk et al. 2002) and relatively short-lived (it is a biennial; Gleason and Cronquist 1993). It may be dependent on short distance dispersal unless water or animals serve as secondary vectors (Cavers et al. 1979). *Ailanthus altissima* is an invasive tree with long-distance seed dispersal, primarily by wind. Seed have been documented to travel as far 200 m (Kota 2005) or further; other wind dispersed plants have seed dispersal distances as far as 300 m (Robinson and Handel 1993). This tree is dioecious and clonal, spreading via root suckers (Gleason and Cronquist 1993) and is often associated with disturbed habitats in high light (Hu 1979, Hamerlynck 2001). *Rhamnus*

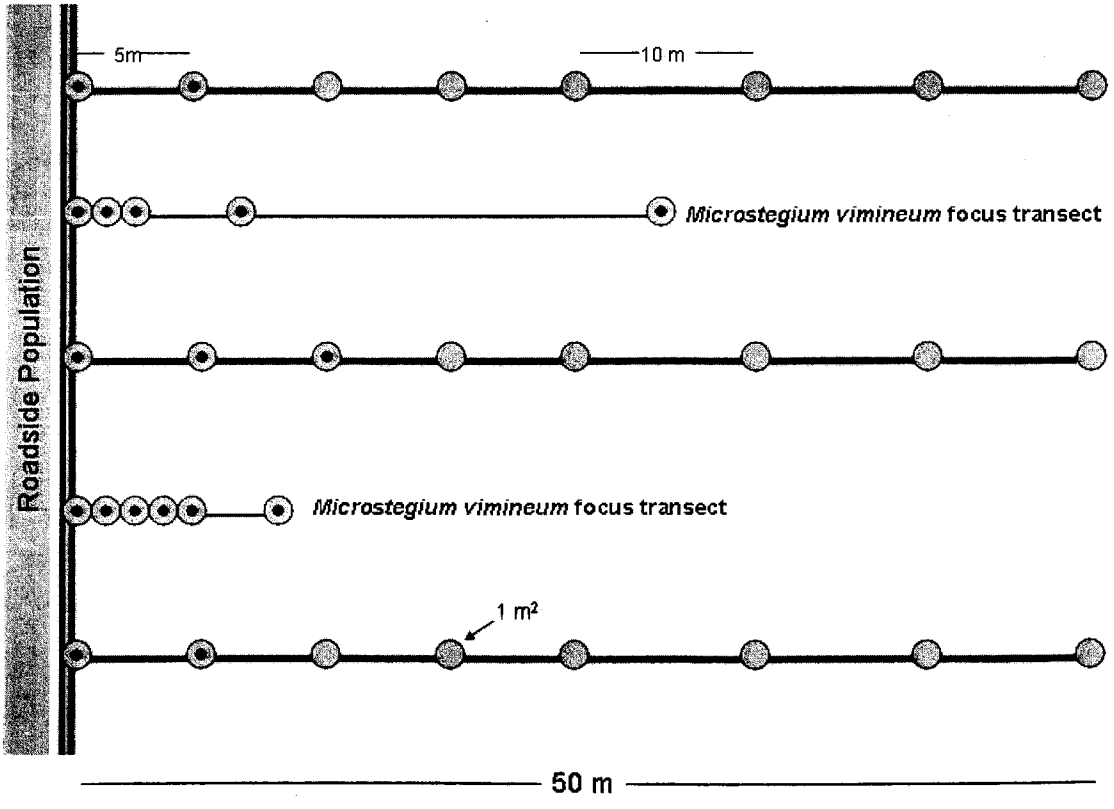
Table 1. Comparison of the five invasive species in terms of three key invasive plant traits. + indicates that the trait is well-documented in the literature and – indicates that the trait is not documented.

Plant Trait	Shade-tolerance	Prolific long-distance seed dispersal	Clonal growth
Microstegium vimineum	+	—	—
Alliaria petiolata	+	—	—
Ailanthus altissima	—	+	+
Rhamnus cathartica	—	+	—
Celastrus orbiculatus	—	+	+

cathartica is non-clonal shrub or small tree that may sucker (Gleason and Cronquist 1993) from its base if cut, but is not clonal. It is dioecious and produces fruit that is bird-dispersed (Godwin 1943) potentially as far as 6 km (Haas 1995). It is found in both high and low light habitats but its growth rate is faster in high light (Harrington et al. 1989). *Celastrus orbiculatus* is a vine that reproduces by seed (Gleason and Cronquist 1993) and vegetatively via root suckers (Dreyer et al. 1987). The fruit are dispersed by birds (Robinson and Handel 1993) or small mammals (Dreyer et al. 1987). This species is imperfectly dioecious with some hermaphroditc and monoecious plants (Hou 1955, Dreyer et al. 1987). While this species germinates readily in low-light environments, growth is slower than plants in high light (Patterson 1975, Greenberg et al. 2001).

Study Site and Design. Sixteen sites in West Virginia, each with roadside populations adjacent to a closed-canopy forest, were sampled in June and September of 2005 and again in 2006. Sampling took place along three perpendicular transects 50 m into the forest interior and two additional transects with a plot located whenever *Microstegium vimineum* was present (Figure 2). Cover of all plant species within each 1 m^2 plot was determined in June. Cover of *M. vimineum*, height of the tallest stem of *M. vimineum* within each plot, and number of chasmogamous (CH) and cleistogamous (CL) inflorescences on that same stem were determined in September. Seed were collected from each flower type from interior and roadside populations near the sample sites. Seed were weighed and tetrazolium viability tests were conducted. Soil (0.001 m^3) was

Figure 2. Sampling design. Circles represent 1 m^2 plots. Circles with nested smaller circles represent plots with *Microstegium vimineum* present. Two transects between the main three were used to estimate the spread front as well as furthest distance, placing plots only where *M. vimineum* was present.



collected just outside of each plot at the same distance and analyzed for its seed bank. Sticky traps were placed just outside of each plot in late September and remained until plant senescence along the main transects in order to determine actual seed dispersal. Light measurements and canopy densiometer readings were taken at every plot over a three hour period of a generally sunny day for each site, and percent bare ground and litter depth were determined. Soils were analyzed for total N and C. Logistic regression analysis was used to determine which variables defined the presence or absence of *M. vimineum* under forested canopies.

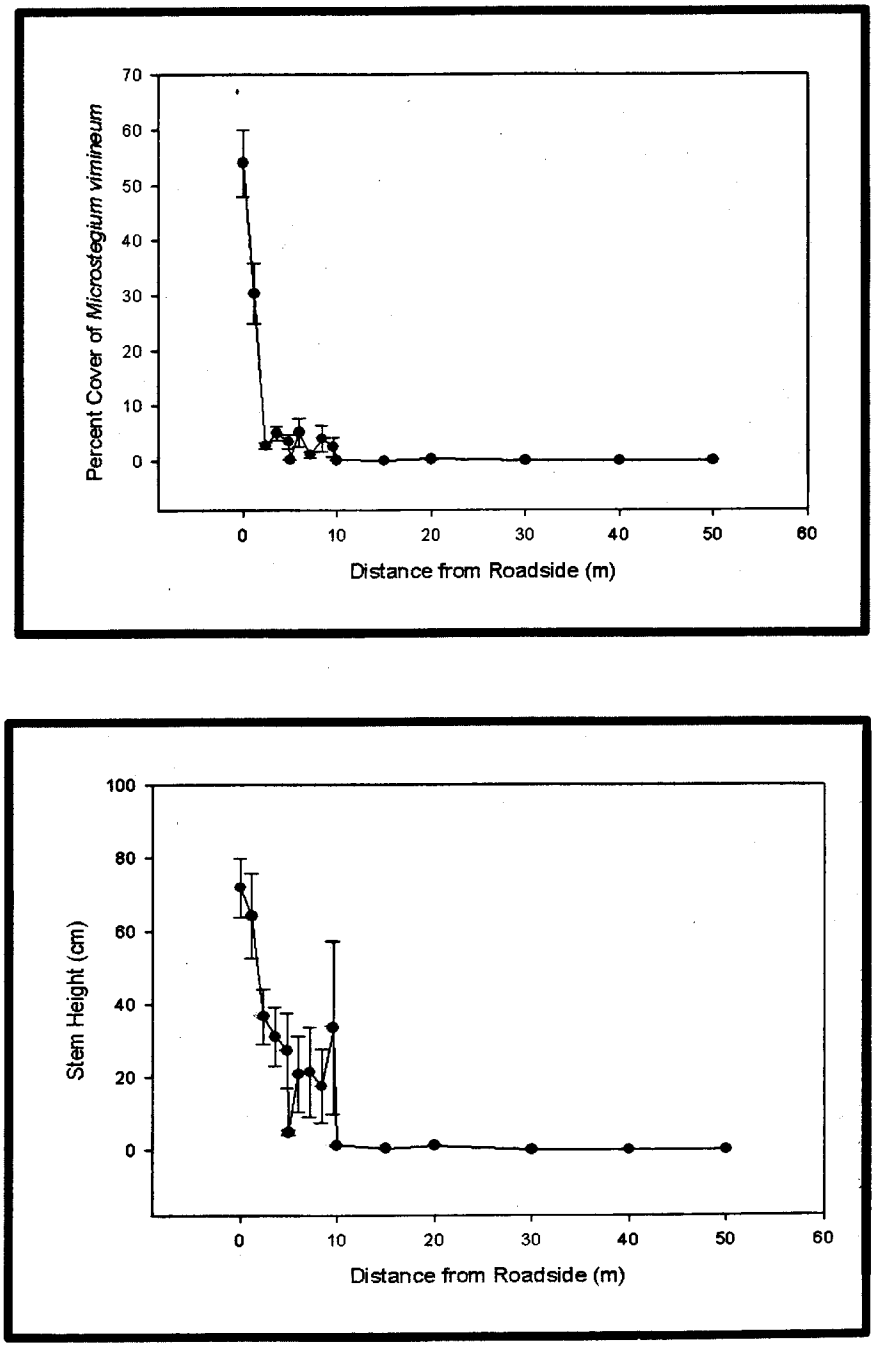


Figure 3. a. Percent cover of *Microstegium vimineum*; b. stem height along the roadside to forest interior gradient (averaged over 16 sites).

Results and Discussion

While *M. vimineum* plants were found as far as 30 m from the road in 2005, most cover was found within 10 m of the roadside (Figure 3a), and stem heights were significantly taller along the roadside compared to distances greater than 5 m into the forested sites (Figure 3b). Seed production, stem height, and cover were significantly correlated with light (possible threshold of 30 ~molm^{-2}s^{-1}) and canopy opening; these findings agree with other studies (Claridge 2002, Gibson et al. 2002). Full CH inflorescences only occurred between 0 - 5 m (Figure 4a). Seeds were not found beyond 1.5 m on the sticky traps and an

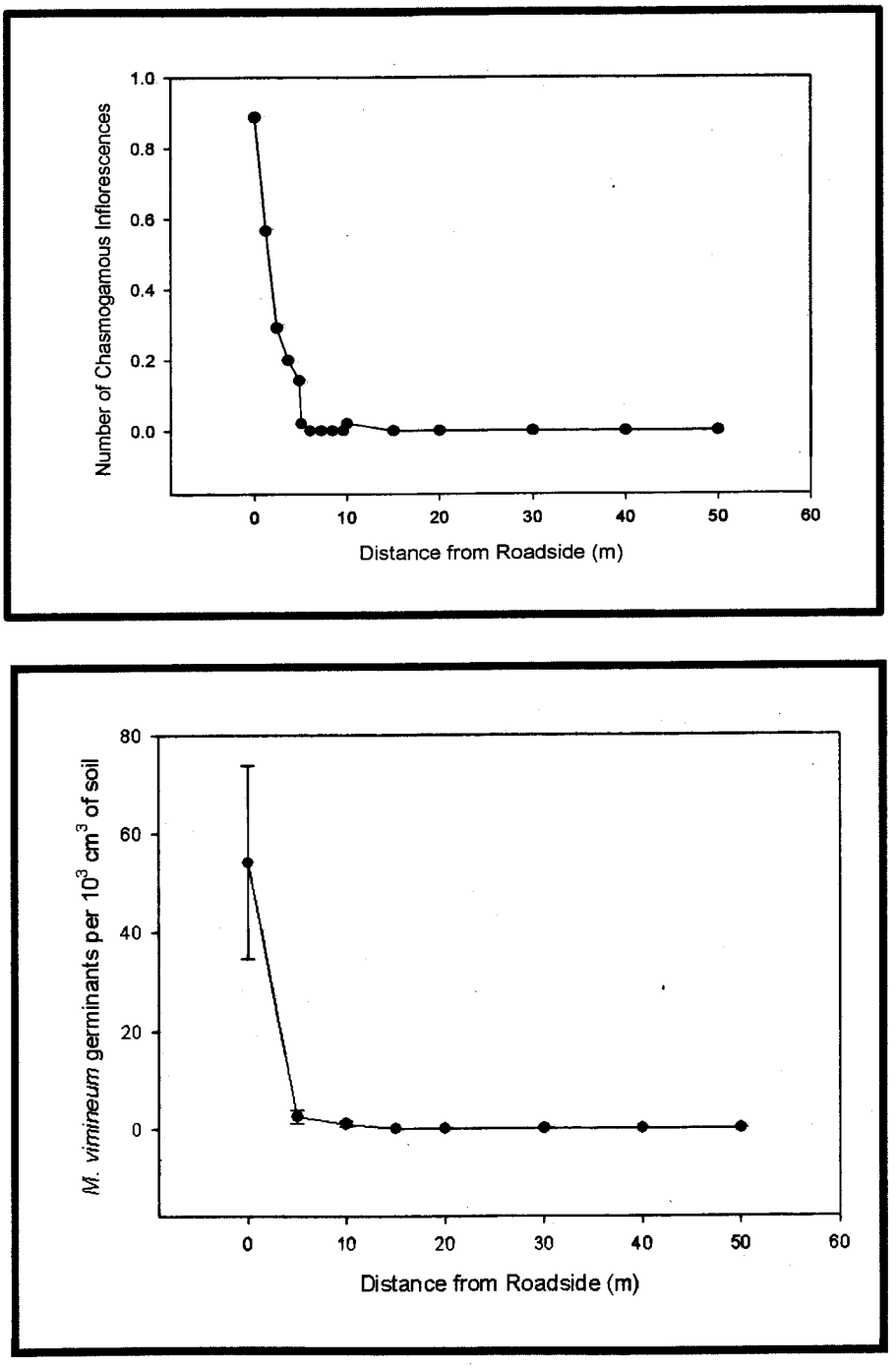


Figure 4. a. Number of chasmogamous flowers and b. germinants from the seed bank of *Microstegium vimineum* along the roadside to forest interior gradient.

average of 24 seeds per site were deposited on the traps, suggesting that most seed remains on or near the plants and that the seed are not wind dispersed. Seed did not germinate from distances beyond 10 m in the seed bank, with a mean of 54 germinants at distance 0 m, 2.44 at 5 m and 0.98 at 10 m (Figure 4b). While interior populations (beyond 5 m) produced far less seed of each type (Figure 5a), the ratio of partially CH+ CH inflorescences to CL inflorescences was larger (Figure 5b). Viability tests showed that interior population

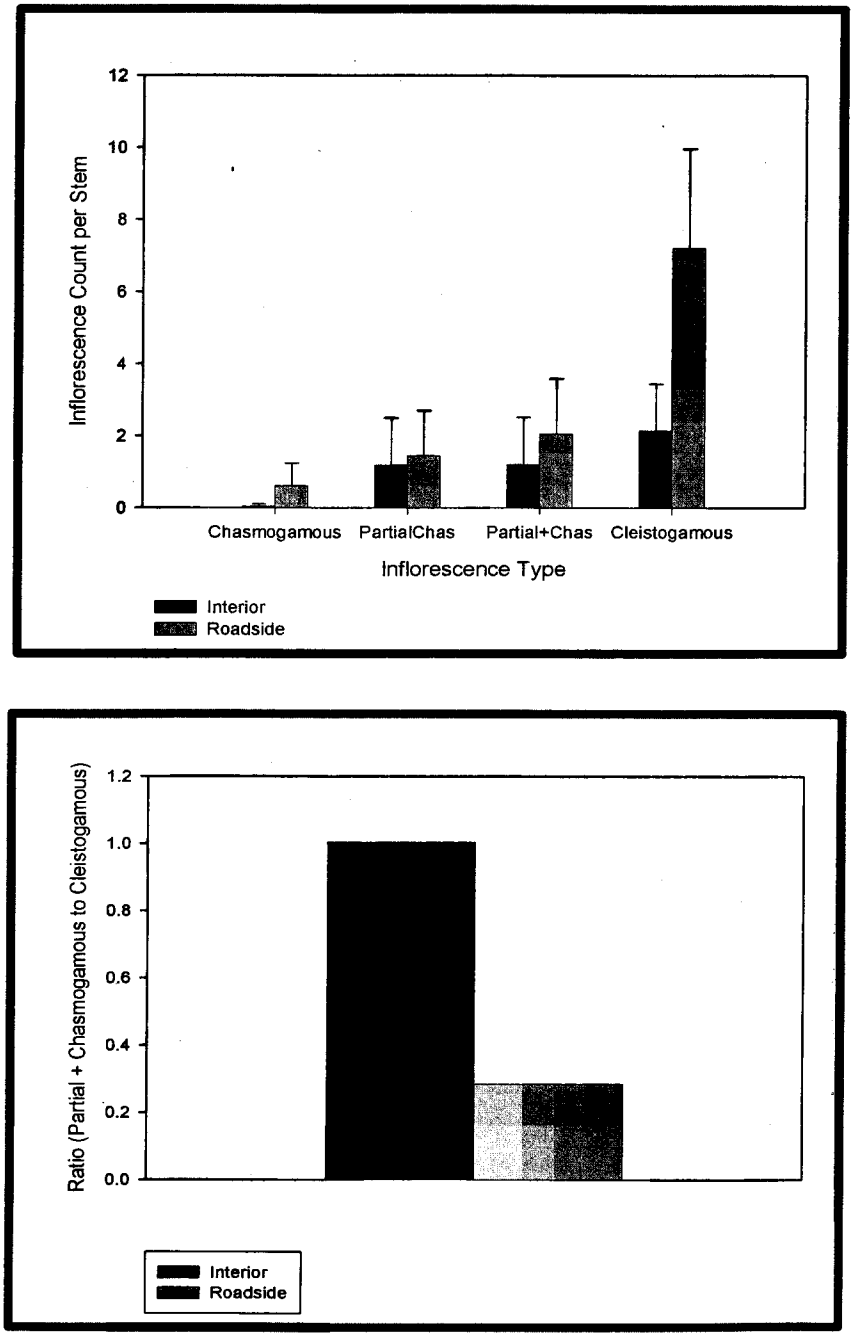


Figure 5. a. Comparison of inflorescence types and b. ratio of inflorescence types between interior (located beyond 5 m into the forest interior) and roadside populations. Partially chasmogamous refers to inflorescences with a few open flowers but mostly closed flowers. PartialChas refers to partially chasmogamous flowers. Partial + Chas indicates a sum of both partially chasmogamous and chasmogamous flowers.

seeds were equally viable to roadside population seeds (CL or CH), and that seeds from CL and interior flowers weighed less than seeds from CH and roadside seeds, respectively. Presence or absence of *M. vimineum* at distances beyond 5 m was significantly related to species richness (richer plots were 39% more likely to have *M. vimineum*), but not to litter depth, amount of bare ground, C:N ratio, or increased canopy opening or light. Because plant spread, cover, and seed production are significantly lower under shaded environments (<30 $\sim mol\,m^{-2}s^{-1}$), such populations may experience an Allee effect and decrease in size (with no new disturbance) or increase more slowly than roadside populations. The Allee effect is a positive relationship between population density and a population's per capita growth rate; i.e., individuals of smaller populations exhibit a decrease in reproduction and a survival. These results suggest that management efforts should focus on roadside populations. The invasive front decreased slightly in distance (0.53 m on average) from the roadside populations between 2005 and 2006 (Table 2). However, the number of individuals found beyond 5 m increased (1.81 new plots on average) as well as the distance of the furthest individuals (47.2 m being the furthest distance and 5.6 m being the average increase), but not significantly. The potential importance of long-distance dispersal by deer and water flow events needs to be determined.

Based on these data, most *Microstegium vimineum* spread will occur along non-forest corridors over short distances; potentially a meter a year. Movement into forested areas will be in cms/yr with greater movement after flood events and via people and deer. The rate of spread by deer, water and other similar sources may increase as the corridor and encroaching understory population increases in size. Focusing on the corridor populations early should reduce directed spread into gaps and the rate of coalescence of interior populations. In contrast, spread of the herb *Alliaria petiolata* along corridors or into forests is likely to be at approximately equal rates (1 – 1.5 m/yr based on average plant heights). Because plant size and seed production do not appear to differ between roadside and interior populations (but this needs confirmation), it is unlikely to suffer from any Allee effect and its spread into forest interiors may be faster than that of *M. vimineum*. Flood events and relatively rare dispersal by people and deer may result in small outlying populations, which are predicted to coalesce more rapidly than those of *M. vimineum*. While all five species may respond positively to forest canopy gaps and other disturbances that increase light, species with long-distance dispersal are likely to benefit the most. Gap formation (due to tree mortality) is estimated to occur at a rate of 1% of the trees per year in temperate forests (Runkel 1985), which could be used to estimate spread rate, especially for plant species whose seed are dispersed by animals attracted to such openings. The shrub *Rhamnus cathartica* will not spread by clonal

Table 2. Comparison of spread of *Microstegium vimineum* (MV) into forest interiors of West Virginia in 2005 and 2006. Numbers are averages over 16 sites. Differences were not significant; standard errors are in parentheses.

Year	Number of plots with MV located beyond 5 m from the roadside	Furthest (m) plot with MV from the roadside	Distance (m) of MV the front from the roadside
2005	2.94 (1.04)	10.9 (2.72)	4.73 (0.85)
2006	4.75 (1.22)	16.3 (2.95)	4.20 (0.55)

growth and is solely dependent on birds/ animals for dispersal. However, dispersal distances will be greater and more selective (to other similar sites and forest gaps), which may make establishment of new reproducing individuals more likely, although research to confirm this is needed. Some studies indicate that bird travel between abundant food sources (open fields and forest edges) is greater than that into forest gaps (Bartuszevige and Gorchov 2006). The spread of *R. cathartica* will also depend on the presence of female trees. Much of *Ailanthus altissima*'s spread will occur along non-forest corridors and slowly into the forest interior. Dispersal will occur over long distances, but seeds may be less likely to find optimal sites. *Ailanthus altissima* will be able to respond quickly to a disturbance and these new populations, if female trees are present, will produce seed that can travel long distances. *Celastrus orbiculatus* will spread along corridors, slowly into forest interiors, and by birds or mammals over long distances into forest gaps and along new corridors. The directed dispersal, its ability to spread clonally, and its use of perfect and monoecious reproductive strategies may make this species the fastest spreading of the five taxa. However, more information about bird preferences for the fruit and successful establishment after dispersal is needed to confirm this prediction.

Microstegium vimineum and *Alliaria petiolata* may have greater local impacts on native forest vegetation despite being relatively limited in initial spread rates, but this impact is likely to be reduced more effectively by focusing on the corridor populations. However, because of the possible local Allee effect in *M. vimineum* populations, it may be possible not only to slow the spread of this species but eradicate it locally. The apparent lack of such an Allee effect in *A. petiolata* and the long distance dispersal of the other three species make focusing both on the source populations and the satellite populations a must if eradication is sought. Slowing the spread of the species with long-distance dispersal may be best done at a landscape scale, focusing on the satellite populations and new safe sites (new disturbances) where plants are more likely to become established. Unless all corridors over a very large area can be treated, focusing on the corridors will not prevent spread of species with long-distance dispersal into forests and back into the previously treated sections of corridor.

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