

Decoupling litter barrier and soil moisture influences on the establishment of an invasive grass

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Abstract

Background and aims Through recruitment, plants establish in novel environments. Recruitment also is the stage where plants undergo the highest mortality. We investigate the recruitment niche for *Microstegium vimineum*, an annual grass from East Asia spreading throughout eastern North American forests.

Methods Current observational and greenhouse research indicates that *M. vimineum* recruitment may be inhibited by leaf litter and promoted by soil moisture; we use field studies to experimentally test how these factors influence *M. vimineum* germination, seedling survival and reproduction. Specifically, we introduce *M. vimineum* seeds into forest microhabitats

with experimentally varied levels of soil moisture and leaf litter.

Results Soil moisture increases *M. vimineum* germination regardless of leaf litter thickness and ameliorates seedling mortality in deep leaf litter. Seed production per m² increases with watering, reflecting higher germination and survival, whereas per capita seed production increases with leaf litter thickness, reflecting density-dependent limits on seed production. **Conclusions** The interactive effects of varied levels of soil moisture and leaf litter thickness on key *M. vimineum* life history stages highlight the need to consider multiple drivers, such as rainfall and local forest disturbance, when assessing how soil properties influence the establishment of invasive plants.

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Introduction

Plant population establishment and persistence depend on recruitment (seed germination and survival). The habitat requirements for plant recruitment are often narrower than those of adults so that observed species distributions are often shaped by the recruitment niche (Clark et al. 1998; Grubb 1977; Harper 1977; Warren and Bradford 2011). Soil properties, such as moisture and litter layer depth, are key variables influencing the

recruitment success of seedlings and hence the distribution and abundance of vegetation (Albrecht and McCarthy 2009; Oswalt and Oswalt 2007; Warren and Bradford 2011). Specifically, soil moisture is a critical variable in recruitment as desiccation is the major cause of plant seedling death (Engelbrecht et al. 2006; Evans and Etherington 1990, 1991; Lambers et al. 1998; Moles et al. 2003; Padilla et al. 2007). Whereas increased soil moisture promotes seedling recruitment, accumulated leaf litter commonly acts as a barrier against plant recruitment in woodland habitats (Albrecht and McCarthy 2009; Warren et al. 2012; Xiong and Nilsson 1999). There is little information, however, on how soil moisture and leaf litter interact to affect recruitment of native or invasive plants.

Microstegium vimineum is an exotic, annual grass that vigorously invades along roads, waterways and forest edges in the eastern U.S. (Christen and Matlack 2009; Eschtruth and Battles 2009; Warren et al. 2011a, b). Its invasion has been linked to declines in native species diversity, tree recruitment, and soil carbon stocks (see Warren et al. 2011b and references therein), highlighting the need to understand the factors that facilitate its establishment to project future impact and inform management. *Microstegium vimineum* invasions are most pronounced at higher soil moistures (Droste et al. 2010; Warren et al. 2011a), but it is uncertain whether this association is because higher moisture facilitates its recruitment (Warren et al. 2011a) or because *M. vimineum* plants increase soil moisture through ground-level shading (Ehrenfeld et al. 2001; Nagy et al. 2011). Also, at higher soil moistures, *M. vimineum* exhibits higher seed production, which may overcome desiccation barriers to recruitment success (Bazzaz et al. 2000; Gallagher and Fuerst 2006; Warren et al. 2011a). The experimental manipulation of soil moisture in ecologically realistic field conditions is necessary to unambiguously determine whether soil moisture is an important regulator of *M. vimineum* recruitment. Similar manipulations are required for leaf litter because, although accumulated leaf litter appears to act as a barrier against *M. vimineum* recruitment (Schramm and Ehrenfeld 2010; Warren et al. 2011a), *M. vimineum* invasion may promote soil chemistry changes that decrease leaf litter (Chesson et al. 2004; Elgersma et al. 2012; Kourtev et al. 1998, 2002a, b). As such, the observed associations between *M. vimineum* success and reduced leaf litter may be an impact of *M. vimineum*

colonization rather than a promoter of *M. vimineum* establishment.

Understanding the role of soil moisture and litter depth in plant recruitment is further complicated by the fact that some species reduce recruitment failure by producing persistent seeds which remain dormant through poor conditions so that a seed bank remains for better periods (Evans et al. 2007; Gallagher and Fuerst 2006). As with many “weedy” species (Gallagher and Fuerst 2006), *M. vimineum* is a prolific seed producer and can establish a substantial seed bank (Claridge and Franklin 2002; Gibson et al. 2002; Horton and Neufeld 1998). *Microstegium vimineum*’s seed bank appears to persist through drier conditions, complicating the interpretation of observed relationships between its presence and soil moisture.

The interactions among environmental factors (e.g. soil moisture, litter depth) and recruitment requirements necessitate experimentation to decouple the impacts on plant establishment (Boyd and Van Acker 2004; Gallagher and Fuerst 2006). This need is especially true for plants such as *M. vimineum* that potentially alter soil moisture and litter decay, and produce seed banks. Where it is known that *M. vimineum* invasion correlates with higher soil moisture and reduced leaf litter (Cole and Weltzin 2004; Ehrenfeld et al. 2001; Elgersma et al. 2012; Kourtev et al. 1998, 2002b; Nagy et al. 2011), how soil moisture and leaf litter jointly influence *M. vimineum* establishment is unknown and needs to be decoupled. Ethical considerations about introducing invasive species in novel habitats, and the logistical difficulties inherent in field experimentation, have limited such investigations. To address this question, the impacts of soil moisture and leaf litter need to be decoupled from one another. For these reasons, we use controlled field studies with experimental manipulation of soil moisture and leaf litter thickness to elucidate the mechanisms driving *M. vimineum* recruitment. We added *M. vimineum* seeds to previously uninvaded forest habitat, using PVC collars to prevent uncontrolled invasion by the exotic grass, and we ask how manipulating leaf litter thickness and soil moisture affects *M. vimineum* recruitment (germination, survival and seed banking) and subsequent reproduction (seed output). Given that *M. vimineum* thrives in mesic habitats (Cheplick 2010; Claridge and Franklin 2002; Cole and Weltzin 2005; Flory et al. 2007; Morrison et al. 2007; Warren et al.

2011a), we expect greater germination, seedling survival and reproduction with higher soil moisture. Whether thicker leaf litter overwhelms the benefit of high soil moisture on germination and survival is uncertain. We expect that thicker leaf litter will inhibit *M. vimineum* germination and survival, even in higher moisture availability (Glasgow and Matlack 2007; Marshall and Buckley 2008; Oswalt and Oswalt 2007; Warren et al. 2011a, 2012), but several studies have found leaf litter an insufficient impediment to *M. vimineum* recruitment and invasion (Cole and Weltzin 2004; Schramm and Ehrenfeld 2010; Warren et al. 2012).

Methods

Study site and plot design

We established six blocks in Sept. 2009 in the Nantahala Forest, Jackson County, North Carolina, USA (35°17'10"N, 83°17'27"W, 777–790 m elevation). The area was unoccupied by *M. vimineum* for at least nine years of direct observation and likely was never occupied. The site contained a mid- to mature oak-hickory-maple community with acidic clay soils typical of mesic forests in the region, but was located on a small rise at a forest edge. Within each 0.24-m² plot, six 15-cm long × 10-cm dia (78 cm²) PVC collars ("plots") were embedded in the soil in a 2 × 3 arrangement (Append. 1), giving a total of 36 treatment plots (6 blocks × 6 plots). To ensure that the locations and treatments did not include unintentional *M. vimineum* seed, an identical block of plot replicates was set up alongside each block (6 plots with treatments in 0.24-m² plots) lacking any *M. vimineum* seed addition. These were not included in analysis as they were only used to assess potential site and treatment contamination.

All treatment plots received 16 *M. vimineum* seeds in Sept. 2009. Seeds were harvested from a local population at the Coweeta Long Term Ecological Research site (CWT) in Macon County, NC, USA (35°03'N, 83°25'W; 685 m elevation). To prevent unintentional *M. vimineum* seed input and seed predation after seed addition, all plot PVC collars immediately were covered with 1-mm² pore screen mesh (secured with a metal clamp). The PVC collars, screens and clamps were removed in early May 2010 to minimize any effects on plant germination or growth.

Experimental treatments

The six blocks were located across a north-facing forest edge to create a light gradient. Across this edge, blocks were clustered so that two blocks were 4 m inside the forest, two were 2 m inside the forest and two were at the forest edge. This created an understory light gradient (mean ± SE): 11 ± 9 %, 15 ± 7 %, 22 ± 7 % (pre-canopy leaf out = 72 ± 8 %, 77 ± 6 %, 81 ± 3 %), respectively. These levels were determined using the methodology outlined below in 'abiotic monitoring'.

Leaf litter within the plots was manipulated to three levels: bare soil (Lt1); decomposed leaf litter from previous years that resided as a shallow (~1 cm depth) crust on top of the forest soil (Lt2); and additional to the previous year's litter, 5 cm (depth) of the current year's leaf litter (Lt3). Seeds were placed on the bare soil (Lt1), on decomposed leaf litter (Lt2) or between decomposed and current litter (Lt3). The litter mostly consisted of deciduous tree leaves typical of the forest (e.g., *Carya* spp., *Quercus* spp., *Acer* spp.). This methodology mimicked *M. vimineum* falling on disturbed soil, undisturbed soil without concurrent leaf litter accumulation and undisturbed soil with concurrent leaf litter accumulation. Untreated water was delivered via drip irrigation (Dripworks, Inc., Willits, CA, USA) to half ($n=6$) the plots in each block weekly (for 2 h, at 4 Lh⁻¹ flow) across March–August 2010. Drip irrigation has a limited moisture shadow, and it raised soil moisture in targeted plots by ca. 10 %. Plots were not watered and litter was not manipulated in 2011.

Abiotic monitoring

Temperature, soil moisture and diffuse light were measured at each block monthly March–August 2010 and averaged by block. Temperature was measured by placing a HOBO U23 Pro v2 Temperature/Relative Humidity datalogger (Onset, Cape Cod, Massachusetts, USA), in the center of each block. The dataloggers were positioned 15 cm above the ground beneath a wood radiation shield. Percent photosynthetically active radiation (PPFD, diffuse light) was calculated as the difference between plot-level PAR readings and a fully exposed PAR reference site. The understory measurements were taken with an LI-191 line quantum sensor and the open reference measurements were taken with an LI-200 spherical PAR sensor and logged with a LI-1400 datalogger (LiCor, Inc.,

Lincoln, Nebraska, USA). Measurements were taken during early morning (8–9 a.m.) to minimize relative error in diffuse light. Volumetric soil moisture (%) was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific Inc., Logan, Utah, USA) in each plot.

Plant demography

Germination was recorded as the number of seedlings – from the 16 seeds added to each plot – appearing in May 2010. Survival was calculated as the proportion of these seedlings persisting to Oct. 2010. In Oct. 2010, growth was calculated as per capita biomass (as annuals, growth only occurs during 1 season) and reproduction was recorded as the number of seeds produced. The adult plants were harvested, the seeds removed and all plant matter was dried for 1 week at 60 °C before weighing. We harvested the plants before any seeds were dropped, so no biomass was lost, but this precluded a full count of all potential seeds. However, existing evidence suggests *M. vimineum* plant biomass, seed number and seed biomass are highly correlated (Warren et al. 2011a, 2012). We evaluated our data for these parameters in a covariance matrix and found them highly covaried ($r=0.77–0.95$). For these reason, we did not evaluate *M. vimineum* growth, seed number and seed biomass as independent demographics; instead we used seed number as an intuitive indicator of fitness for an annual grass (Evans et al. 2007). *Microstegium vimineum* produces both outcrossed and self-fertilized seeds (Cheplick 2005, 2006), but we considered total seeds as Cheplick (2007) cautions about making inferences from the proportion of outcrossed seeds, and self-fertilization does not appear to impact fitness in annuals (see Morgan 2001). The plots were surveyed again in June 2011, and the number of emerging *M. vimineum* plants was scored.

Data analysis

We used generalized linear mixed models to evaluate the fixed effects (watering and litter layer thickness) on *M. vimineum* germination, survival, reproduction and seed bank. Because previous work (Warren et al. 2012) suggests density-dependent limits on individual *M. vimineum* reproduction, we evaluated per capita seed production as a function of surviving plant density. Generalized linear mixed models allow robust

analysis of observational and experimental ecological data that often violate classical statistical assumptions of normality and independent variance among collars (Bolker et al. 2009). We coded watering as categorical, 0 and 1, and litter as 0, 1 and 5 cm as these were biologically meaningful. The response variables were evaluated as binomial proportions (binomial error distribution) except per capita, total and density-dependent reproduction (Poisson error distribution). We account for potential spatial autocorrelation, and the influence of ambient abiotic heterogeneity, by evaluating ambient light temperature and soil moisture along with block as random effects. This approach is similar to ‘blocking’ in a factorial design, but can detect variation in the abiotic gradients otherwise considered unobserved error in block effects (Bolker et al. 2009). The mixed models were fit using the Laplace approximation in the “lme4” package (Bates and Maechler 2009) for the R statistical programming environment (R Development Core Team 2012). The inclusion or exclusion of random effects was based on Akaike’s Information Criterion (AIC) values (Akaike 1973). Random effects were included when $\Delta\text{AIC}<2.0$. There was no collinearity in any models (variance inflation <2), and overdispersion in the binomial and Poisson error distributions was relatively low (<5), particularly for ecological data (see Zuur et al. 2007). Because overdispersion was high in the total seed production model (>20), we used a lognormal Poisson model with individual-level random effects (e.g., Elston et al. 2001). We evaluated the slope value of the fixed effects and considered coefficients with p -value <0.05 significant and coefficients with p -value <0.10 marginally significant (sensu Hurlbert and Lombardi 2009).

Results

Mean (\pm SD) summer (May–Sept. 2010) temperature at the study site was 20.9 ± 0.6 °C, diffuse light was 16.0 ± 0.5 % and mean ambient soil moisture was 32.7 ± 5.6 %. We introduced 576 *M. vimineum* seeds and 55 % germinated across all plots and treatments. Of those that germinated, 87 % survived to become reproductive adults. The reproductive adults produced 1,488 seeds, 2.5 times as many as we initially added, a conservative estimate since we harvested early during seed set. Whereas 45 % of the seeds did not germinate in the first

year, 6 % of the initial seeds (or 13 % of the remaining seeds) germinated from the seed bank the second year (we removed all seeds produced in Oct. 2010 and so they were not part of the seed bank experimentally established in 2009).

We used AIC comparisons to select mixed models with the fewest random effects needed to explain the data. In all models, a single random effect better fit the data than any combinations of block, diffuse light, temperature and soil moisture. Including the abiotic effects did not improve model fit considerably more than including the block effect for any of the models except reproduction, which included block, soil moisture and light (Append. 2). Because block explained variation as well as the measured abiotic variables, and the abiotic variables did not differ greatly, we used block as the random effect in all models to account for the unobserved variation between blocks.

Germination decreased significantly with litter thickness ($coeff. = -0.159$, $SE=0.040$, $p\text{-value}<0.001$) [Fig. 1a] and increased significantly with watering ($coeff. = 0.384$, $SE=0.172$, $p\text{-value}=0.026$) [Fig. 1b], and there was no interaction. For survival, however, a marginally significant interaction term indicated that watering ameliorated the negative impact of increased leaf litter thickness on seedling persistence ($coeff. = 0.291$, $SE=0.168$, $p\text{-value}=0.084$) [Fig. 2].

Total seed production (seeds m^{-2}) did not vary with leaf litter thickness ($coeff. = 0.062$, $SE=0.065$, $p\text{-value}=0.343$) [Fig. 3a], but increased significantly with watering ($coeff. = 0.593$, $SE=0.278$, $p\text{-value}=0.034$) [Fig. 3b], and there was no interaction. Per capita seed

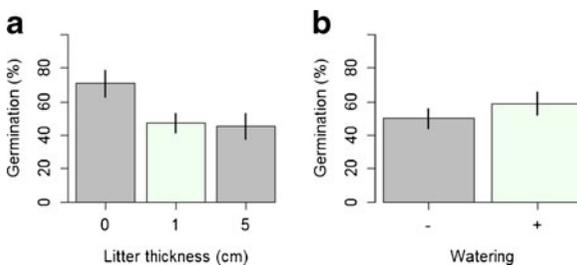


Fig. 1 Mean (\pm SE) treatment effects of leaf litter thickness (a) and watering (b) on *Microstegium vimineum* germination. *Microstegium vimineum* germination only increases significantly where no leaves were added (a) and, regardless of leaf thickness, where the seeds were watered (b). The experiments included the addition of 16 *M. vimineum* seeds on substrates of bare soil, decomposed leaf litter from the previous year and the previous year's litter +5 cm of the current year's leaf litter in watered (+10 % soil moisture) and unwatered plots

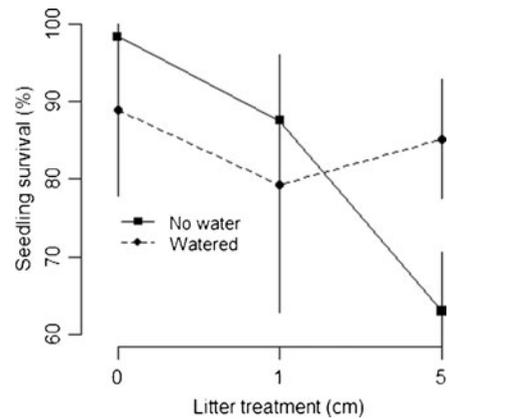


Fig. 2 Interaction plot showing the effects of leaf litter and watering treatments on mean (\pm SE) *Microstegium vimineum* seedling survival. Watering makes no difference in mean *M. vimineum* survival when there is no leaf litter (0 cm) or the previous year's leaf litter (1 cm); however, in the thickest leaf litter (5 cm), watering significantly improves plant survivorship. Lines between points are shown to clarify trends, not to suggest interpolation across points

production increased significantly with leaf litter thickness ($coeff. = 0.104$, $SE=0.032$, $p\text{-value}<0.001$) [Fig. 3c] and increased significantly with watering ($coeff. = 0.353$, $SE=0.147$, $p\text{-value}=0.016$) [Fig. 3d],

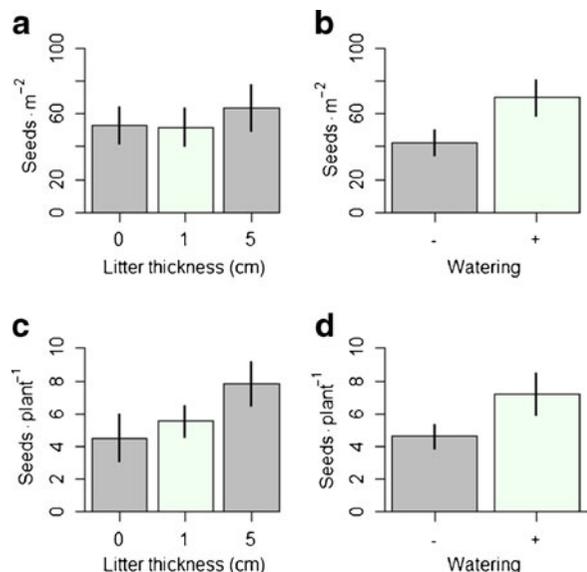


Fig. 3 Boxplots showing mean (\pm SE) treatment effects of leaf litter thickness (a, c) and watering (b, d) on total reproduction (seeds m^{-2}) and per capita reproduction (seeds $plant^{-1}$). Litter thickness had no effect on total seed output (a) but it did increase significantly with watering. Seeds per plant increased significantly with leaf litter thickness (c) and watering (d)

and there was no interaction. The reproduction effects appeared to be density-dependent so we evaluated the correlation between per capita seed production and plant density and found that per capita seed production decreased significantly with plant density ($coeff. = -0.059$, $SE=0.020$, $p\text{-value}=0.003$)

A significant interaction term indicated that the proportion of 2011 seedlings emerging from *M. vimineum* seeds added in 2009 only decreased with watering in the absence of leaf litter ($coeff. = 0.403$, $SE=0.215$, $p\text{-value}=0.062$) [Fig. 4].

Discussion

Forest leaf litter restricts plant recruitment (Belote and Jones 2009; Xiong and Nilsson 1999), including recruitment of *M. vimineum* (Glasgow and Matlack 2007; Marshall and Buckley 2008; Oswalt and Oswalt 2007; Warren et al. 2011a, 2012), yet *M. vimineum* thrives in mesic forests across broad spatial scales (see Warren et al. 2011a and references therein). Warren et al. (2012) showed that *M. vimineum* could overwhelm leaf litter with propagule pressure, but did not explore how variation in litter depth and soil moisture influenced *M. vimineum* establishment. By introducing seeds and manipulating both leaf litter and soil moisture under realistic ecological conditions, we decouple cause and effect – at least for *M. vimineum* recruitment – to demonstrate the plant's dependence on mesic conditions and forest litter disturbance for establishment.

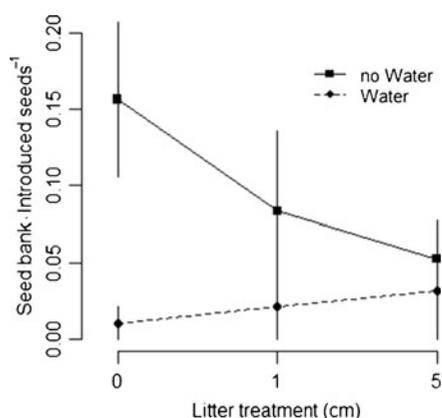


Fig. 4 Interaction plot showing the effects of 2010 leaf litter and watering treatments on mean (\pm SE) *Microstegium vimineum* seed bank germination in 2011. Significantly more seedlings emerged from the 2010 seed bank with watering only in the absence of leaf litter

We find soil moisture integral for *M. vimineum* recruitment. Leaf litter consistently inhibits *M. vimineum* germination whereas watering increases germination regardless of leaf litter thickness (Fig. 1). Moreover, watering ameliorates seedling mortality in the deepest leaf litter (Fig. 2). The mechanism for this interaction could be that leaf litter suspends the seeds in a drier environment above the soil (Schramm and Ehrenfeld 2010) and so watering ameliorates desiccation induced by a pronounced litter layer. Alternatively, it may be that seeds can tolerate shading or desiccation but not both (Gallagher and Fuerst 2006), or that watering overcomes the light deficit below leaf litter by accelerating its decay. However, because experimental watering began during the germination window, it is unlikely that it promoted enough leaf litter decomposition to impact recruitment via light.

Overall *M. vimineum* seed production increases with soil moisture, but per capita seed production only increased with leaf litter thickness (Fig. 3). The overall increase in seed production in wetter environments further supports the idea that moist habitats are highly conducive for *M. vimineum* persistence and spread, and not simply a result of the plant modifying the moisture environment (e.g. by shading that reduces water loss from the soil). Equally, our experimental manipulations suggest that reduced leaf litter thickness in *M. vimineum* invasions is not simply an invasion effect, but rather a condition that itself promotes *M. vimineum* establishment. Notably, the leaf litter effect on per capita seed production likely is indirect: by reducing germination, leaf litter reduces plant density, which promotes subsequent high per capita seed production. Warren et al. (2012) reported similar density-dependent reproduction effects on *M. vimineum*. The maximum limits on seed output imposed by density-dependence suggests that the ‘treatment’ effect we observe for leaf litter is more a relict of poor initial germination than improved subsequent reproduction. Overall, seed output increased with watering regardless of litter thickness. This result emphasizes that *M. vimineum* appears to have high invasion potential in mesic habitats even at low density because satellite populations can produce copious seed from few individuals, saturating the environment with seed, and potentially overcoming leaf litter limitations (Warren et al. 2012).

We also find evidence that *M. vimineum* seed banking is a strategy for weathering drought (Fig. 4). Germination increases significantly with watering regardless of leaf

litter thickness, and seed banking decreases considerably with watering. As seedling survival also increases with watering regardless of leaf litter thickness, our data support the suggestion that seed dormancy in *M. vimineum* is a strategy for avoiding drought stress and mortality (Gibson et al. 2002; Judge 2008; Webster et al. 2008).

We find *M. vimineum* vegetative and reproductive biomass highly correlated, which has been observed previously (Cheplick 2010; Warren et al. 2011a, 2012). Notably, *M. vimineum* growth and reproduction generally are tightly associated with increased light (see Warren et al. 2011b and references therein), but our focus is on early recruitment, and our light environment (22 % ambient) is much lower than light availability in other studies with less canopy coverage (e.g., Warren et al. 2012), or even full sun (e.g., Flory et al. 2007, 2011). The possibility remains, then, that high light also might overcome leaf litter inhibitions.

By manipulating the environment in ecologically realistic field conditions, we demonstrate that soil moisture directly promotes *M. vimineum* performance and allows the plant to overcome the leaf litter barrier. Both in promoting germination through the leaf litter and in enhancing subsequent seed production, soil moisture makes otherwise unsuitable forest habitat suitable for *M. vimineum* invasion, emphasizing the importance of soil conditions for determining vegetative composition and abundance. These results show how multiple soil dynamics interact – such as that between forest leaf litter and rainfall – so that a single factor cannot be targeted as the sole influence on plant establishment. These are important considerations when assessing invasive species management. Individual environmental factors may not be limiting if they compensate for one another so that one- or two-factor habitat assessment vastly underestimates the causes behind potential invasion.

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