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Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois¹

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GIBSON, D.J., G. SPYREAS, AND J. BENEDICT. (Department of Plant Biology, Southern Illinois University at Carbondale, Carbondale, IL 62901). Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. J. Torrey Bot. Soc. 129:207–219. 2002.—The ecological life history of *Microstegium vimineum*, an invasive grass, was compared among four populations throughout southern Illinois. A detailed investigation of seed production was conducted at one of these populations in a secondary oak-hickory forest in Dixon Springs State Park, Illinois. In this park, *M. vimineum* occurs as a central, main population with several disjunct sub-populations. Size of flowering and non-flowering individuals was determined as the plants set seed. Seed dispersal was assessed using seed traps. A severe late summer drought impacted the Dixon Springs population in 1999 and few plants flowered. Plants that did flower were significantly larger than those not flowering and were limited to one small area at the edge of the core population. At Dixon Springs, the germinable seed bank was estimated from soil samples collected in Fall 1999 before flowering, and in the subsequent spring. Seedlings emerged from soils placed in a greenhouse from samples collected in the spring. No seedlings emerged from samples collected in the fall. Germinable seed had a 10 times higher density in samples collected near the soil surface than from samples collected at 5–10 cm depth. Seed dispersal occurred within the main population only. Despite the lack of seed dispersal in 1999, seedlings emerged from six of seven subpopulations in spring 2000, with the highest densities where plants had flowered in 1999. These data indicate the presence of a persistent soil seed bank for *M. vimineum*. Even following summer drought and discounting spring seedling emergence, the size of the seed bank increased by ~25% in 1999. Reestablishment of the Dixon Springs population following the 1999 drought was vigorous, but the location of the largest, most fecund plants in 2000 was not the same as in 1999. In 2000, end of season survivorship of *M. vimineum* among all populations was 40–50%, with 90% of surviving individuals flowering. Performance of *M. vimineum* varied significantly within and among populations and was related to soil texture and chemistry, and overhead canopy cover. The findings of our study reflect the invasive nature of this plant. A sufficiently large seed bank and a highly plastic morphological response to local microhabitat conditions likely ensures its persistence in invaded sites.

Key words: Annual plants, exotic plants, *Microstegium vimineum*, invasion, life history, seed bank, seed dispersal, seedling establishment.

Microstegium vimineum (Trin.) A. Camus (Eulalia, Japanese grass, stiltgrass, Nepal microstegium) is a grass of Asian origin that was first discovered in the United States in 1919 in Knoxville, TN and is now widespread east of the Mississippi River (Fairbrothers and Gray 1972; Hunt and Zaremba 1992; Redman 1995; Ehrenfeld 1999). *M. vimineum* has recently been reported as invasive in other countries as well (Scholz and Byfield 2000). *M. vimineum* is an annual grass that invades shady streamside forest habitat. It spreads rapidly into disturbed areas

via animals or water dispersal. On fertile mesic sites it is reported to replace ground vegetation within 3–5 years (Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997). A perennial form of *M. vimineum* has been reported in New Jersey (Ehrenfeld 1999), although the identity of these plants have been disputed (Mehrhoff 2000). *M. vimineum* can be considered an ‘invasive colonizer’ according to Davis and Thompson’s (2000) nomenclature for invasive species.

Invasive species are an increasing threat to native plant communities and are a particular concern for park managers (Westman 1990). In Illinois, invasive species make up ~ 28% of the flora and constitute a serious threat to the integrity of natural areas (Illinois Department of Energy and Natural Resources 1994). *Microstegium vimineum* is listed as one of the 25 exotic weeds considered to pose the greatest threat to Illinois forests (Illinois Department of Energy and Natural Resources 1994). Our study was conducted in southern Illinois where it is reported in at least 9 counties and is of special

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concern in a number of state parks and natural areas (Mohlenbrock and Voigt 1959; Mohlenbrock and Schwegman 1969; Shimp 1996).

Understanding the life history of invasive species is a first step for developing methods for their control and management (Shea and Kelly 1998; Parker 2000), but in the case of *M. vimineum* this information is lacking. Previous autecological studies have focused on its photosynthetic responses to shading (Winter et al. 1992; Horton and Neufeld 1998), clonal foraging (Claridge and Franklin in press), and growth and reproduction (Williams 1998).

As an annual grass, *M. vimineum* depends on germination and establishment from seed every year. In areas where *M. vimineum* is well established, a persistent, multi-year seed bank may develop in which viable seed accumulates in the soil over a number of years. Alternatively, a transient seed bank may occur where there is no carry over of germinable seed from one season to the next. If the latter is true, effective control might be possible by limiting seed production. If a persistent seed bank occurs, then seed production in any one year may be relatively unimportant, and control would need to focus upon limiting germination and seedling establishment. Anecdotal accounts suggest that individuals can produce 100–1000 seeds that can persist in the soil for up to 5 years (Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997). Many annual species develop persistent soil seed banks (Thompson and Grime 1979), and this was our expectation for this species. The dynamics of the soil seed bank is an important life history feature for any plant (Fenner and Kitajima 1999; Gibson 2002), but has been inadequately characterized for many exotic species (Luken 1997). Renne et al. (2001), for example, determined that knowledge of the seed bank of the exotic *Sapium sebiferum* would assist in the development of management strategies.

The overall objective of our research was to assess the importance of the soil seed bank for *M. vimineum*, and to compare survivorship, performance, and seed production within subpopulations at a single site and among populations from several sites.

Materials and Methods. **STUDY SITES.** The primary focus for our study was a population of *M. vimineum* at Dixon Springs State Park in Pope County, Illinois. Three additional Illinois populations were located at Bell Smith Springs

and Lusk Creek, in Pope County, and Cove Hollow in Jackson County.

The Dixon Springs (DS: 37°23'N, 88°40'W) study area lies within the greater Shawnee Hills section of the Shawnee Hills natural division of Illinois (Schwegman et al. 1973), and is characterized by plant communities ranging from mature secondary oak-hickory forest to early successional woods. *M. vimineum* infestation is heavy in an early successional dry-mesic woodland encompassing the east half of the park. Intermittent streams dissect the gently sloping area. The area was abandoned from agriculture in the 1960s. The area is dominated by young *Quercus velutina* Lam., *Q. stellata* Wagh., and *Carya* Nutt. spp., with an overstory of *Juniperus virginiana* L., *Cornus florida* L., *Diospyros virginiana* L., and *Sassafras albidum* (Nutt.) Nees. Common shrubs and vines include *Symphoricarpos orbiculatus* Moench, *Lonicera japonica* Thunb., *Toxicodendron radicans* (L.) Kuntze., and *Vitis* L. spp. The *M. vimineum* population at DS occurs within the most xeric plant community observed by us in Illinois.

An initial distribution survey of the *M. vimineum* at DS showed that a dense main population occurs within the interior of the Park, adjacent to a trail. This population is immediately surrounded by small, isolated peripheral subpopulations downslope and away from the trail. Additionally, a few small, scattered subpopulations occurred further south along the Park's entrance trail, isolated from the large interior core population.

The Bell Smith Springs (BS: 37°37'N, 88°40'W) study area is located in the greater Shawnee Hills section of the Shawnee Hills natural division of Illinois. It is characterized by a permanent stream meandering through steep sandstone bluffs. The *M. vimineum* populations were large and well established on the sandy streambanks at this site. The plant was not found to be encroaching upslope, though it had established itself anywhere the water reached high enough to disperse seed, such as on rock outcrops with *Heuchera parviflora* Bartl. var. *rugelii* (Shuttlw.) Rosend., Butt. & Lak., ferns (*Polystichum acrostichoides* (Michx.) Schott., *Asplenium platyneuron* (L.) Oakes, *Woodisia obtusa* (Spreng.) Torr.), mosses and liverworts. Focal populations occurred in dense vegetation growing on the banks and sand bars of the stream. Co-occurring species included *Andropogon gerardii* Vitman, *Sambucus canadensis* L., *Alnus serrulata* (Ait.) Willd., *Betula nigra* L.,

Corylus americana Walt., *Dicanthelium clandestinum* (L.) Gould, *Platanus occidentalis* L., *Salix* L. spp., *Cassia marilandica* L., *Perila frutescens* (L.) Britt. and *Polygonum* L. spp. Tree canopy was minimal, however shading occurred from steep surrounding slopes.

Cove Hollow (CH: 37°64'N, 89°28'W) is in the southern section of the Ozark natural division of Illinois. *M. vimineum* subpopulations occurred in the rocky streambed of an ephemeral stream within a dense mesic, cove forest. The forest is dominated by *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., *Quercus rubra* L., *Juglans nigra* L., and *Lindera benzoin* (L.) Blume, with *Platanus occidentalis*, and *Acer rubrum* L. occurring adjacent to the stream. Subpopulations were scattered, and no individuals were found outside the cobble/sand streambed.

The Lusk Creek Wilderness Area (LC: 37°37'N, 88°48'W) is a creek habitat similar to that of CH, within the greater Shawnee Hills section of the Shawnee Hills natural division of Illinois (Ashby 1968). The stream is ephemeral, very rocky and surrounded by steep sandstone slopes. The dense forest canopy at LC where *M. vimineum* occurred is dominated by *Quercus alba* L., *Q. rubra*, and *Ostrya virginiana* (Mill.) K. Koch. Associate species included *Lindera benzoin* and *Zizia aurea* (L.) Koch. *M. vimineum* did not appear to be spreading out of the creek bed and the population consisted of scattered subpopulations.

MEASUREMENT OF SUBPOPULATIONS AT DIXON SPRINGS. Seven subpopulations of *M. vimineum* were studied at DS in 1999–2000. Subpopulations 1 and 2 were small and adjacent to a trail, and they likely originated from seed brought in by pedestrian traffic, or grading tractors. Subpopulation 3 was the large, interior, 'core' patch of individuals. Subpopulations 4–7 were small areas peripheral to subpopulation 3. On 24 September 1999, the length and width of all subpopulations were measured to estimate their size. The areal extent of subpopulation 3 was also delineated using metal stakes around the edge of the subpopulation at 20° compass bearings. A visual estimate of percentage cover of *M. vimineum* within each subpopulation, along with presence of co-occurring vascular plants was taken. Overhead canopy cover was measured using a spherical densiometer, taken in the four cardinal directions, in the center of all subpopulations (except for the very large subpopulation 3, where no densiometer measurements

were taken). Densiometer readings were also taken directly outside subpopulations for shade comparisons between invaded and noninvaded areas.

GERMINABLE SEED BANK SAMPLING. Soil samples were collected before anthesis from within and outside *M. vimineum* subpopulations at DS on September 11 1999. Four (12.5 X 12.5 cm) soil samples from the upper (0–5 cm) and lower (5–10 cm depth) soil horizons were taken randomly within each of the seven subpopulations. Four samples were also directly outside and downslope of each subpopulation, for an inside subpopulation/outside subpopulation comparison ($n = 16$ soil samples per subpopulation). All soil samples were cold treated for 5 weeks at 10 C°. Samples were placed in a greenhouse (October 18) in randomly arranged 12.5 X 12.5 cm plastic flats. Obvious root fragments and stones were removed. Control flats containing sterile soil were interspersed with the samples to test for greenhouse seed contamination. Samples were rotated periodically to control for heterogeneity in environmental conditions within the greenhouse. Trays were watered as needed and fertilized monthly with N-P-K (20–10–20). To initiate subterranean seed germination, in March 2000, the soil surface in all flats was lightly broken up and stirred with a tongue depressor to break a crust that had developed. Germinable seed was determined by counting and then removing emerged seedlings from the flats.

The seed bank study was repeated by collecting a second set of soil samples on 26 March 2000. The sampling procedure in subpopulation 3 was modified slightly to incorporate the very small area of fecund plants. Subpopulation 3 soil samples were taken within the small group of flowering plants. Additional samples were taken from subpopulation 3, but >1 m from the group of plants that flowered.

SEED DISPERSAL SAMPLING. Thirty-four seed traps were placed within and outside of the 7 *M. vimineum* subpopulations at DS during anthesis (25 September 1999), and collected after seed shed (15 December 1999) to estimate seed rain. Two seed traps were each placed randomly within subpopulations 1, 2, and 4–7, whereas ten traps were placed within subpopulation 3. Two additional traps were placed directly outside and downslope of each subpopulation to estimate the extent of seed rain.

The traps consisted of plastic plates (201 cm²) coated with Tanglefoot[®] adhesive. Traps were

held secure in the soil by nails. *M. vimineum* seed collected within traps was tested for viability using Tetrazolium on excised embryos (0.1% 2,3,5-Triphenyltetrazolium Chloride) (Grabe 1970).

SEEDLING DENSITY. The densities of *M. vimineum* seedlings germinating in 2000 were estimated in May 2000 by counting the number of seedlings in 1 m radius circular plots centered on the permanent plot marker in subpopulations 1, 2, and 4–7 at DS. Seedling densities were also counted outside of the 7 subpopulations where soil seed bank samples were collected. In subpopulation 3, seedling density was counted in five 1m-radius plots. One plot was located in the center of the 1999 flowering area, a second was located at random in a gully, a third was located in the area of high 1999 *M. vimineum* density (non-flowering plants), and in two additional areas located at random.

PLANT MORPHOLOGY. In 1999, flowering of *M. vimineum* occurred at DS only in a small area within subpopulation 3 and we measured morphological characteristics of these flowering plants. Seed production was assessed by counting seed on 20 of these plants surveyed at random before seed shed (1 October 1999). These plants were compared with 20 plants chosen at random from outside the group of plants in flower, but within subpopulation 3. The following measurements were taken: the number of cleistogamous and chasmogamous inflorescence's (see Ehrenfeld 1999), spikelets, seeds (number and percentage viability), tillers, prop roots, leaves (functional and immature), and nodes, length (sum of all tiller lengths), biomass (g dw at 80 ° C) of the whole plant, the spikelets with seed, and total biomass of all seed.

POPULATION COMPARISON IN 2000. In each population, five transects were located where *M. vimineum* occurred. At DS, one of these transects (transect A) was located within the high-density flowering subpopulation of the 1999 survey. Each transect was 3–5 m in length. Along each transect, ten plants were selected using a stratified random approach and tagged with colored wire ($n = 50$ marked plants per population). The DS population was marked on 18 May 2000 (day 138 of 2000), the CH population on 24 June (day 175), BS on 22 July (day 203), and LC on 10 September (day 253). The number of leaves, tillers and plant length was initially recorded upon marking and was periodically re-

corded after that for a total of 3–5 observations per plant. The most extensive set of measurements were made on the DS plants, which were measured on days 138, 196, 238, 294, and 321. Measurements at the other populations were on days 175, 237, 294, and 321 at CH, days 203, 272, 294, and 321 at BS, and days 253, 294, and 321 at LC. By 17 November (day 321), all populations had flowered and individual plants were starting to senesce. Where possible, the suspected reasons for mortality was noted (e.g., herbivory, pathogens) when plants were found to be dead. On 21 October (day 294), two plants were selected at random from each transect at each site and were collected for additional measurements. The remaining plants (up to 8 per transect) were collected on day 321. In addition to leaf number, tiller number and length, the number of inflorescences, spikelets, nodes and seeds, and biomass (g dw after drying for > 24 hr at 80 ° C) of the whole plant and seed were recorded at days 294 and 321.

A composite soil sample was taken from each transect in October, 2000. Eight-ten sub-samples were collected from 2–10 cm depth along each transect using a soil corer and composited to obtain an approximately 250 g sample. The samples were sent to A & L Laboratories (Memphis, TN) for analysis of pH, extractable P, K, Ca, Mg, percentage organic matter, cation exchange capacity (CEC), and texture (hydrometer method). Overhead tree canopy cover was estimated in mid-summer above each transect at the BS and LC populations using a spherical densiometer.

DATA ANALYSIS. Data on *M. vimineum* plant traits from 1999 at DS were analysed using a 1-way ANOVA testing the effect of location (inside versus outside the flowering patch, $df = 1$) on log transformed dependent values. The different starting dates for observations of each population precluded a valid statistical analysis of the measurements taken on marked plants at the four populations (BS, CH, DS, and LC) through the course of the 2000 field season. These data were examined by simply plotting means and standard errors of mean plant performance (numbers of tillers and leaves, and total stem length) on each sample date. However, a complete set of data were available for plants collected on days 294 and 321 and these data were analyzed using a three-way ANOVA testing the effects of population ($df = 3$), transect nested within population ($df = 13$), date ($df = 1$) and the population-by-date interaction ($df =$

Table 1. Characteristics of *Microstegium vimineum* subpopulations at Dixon Springs State Park. Subpopulation dimensions were measured as length by longest orthogonal width. N/a = measurement not taken.

Characteristic	Subpopulation						
	1	2	3	4	5	6	7
<i>M. vimineum</i> cover (%)	85	95	75–100	35	65	70	65
Dimensions (m)	5.8 × 3.7	9.9 × 3.7	193 × 86	0.9 × 2.5	4.8 × 2.9	7.1 × 3.7	3.4 × 6.8
Area (m ²)	21.7	36.5	16,706.0	2.3	14.0	26.2	23.0
Overhead canopy cover (%) Fall, 1999							
Inside subpopulation	90.6	80.2	N/a	82.3	91.7	95.8	88.6
Outside subpopulation	90.6	86.5	N/a	87.5	89.6	93.7	90.6
Overhead canopy cover (%) Spring, 2000							
Inside subpopulation	N/a	N/a	89.6	95.8	96.9	96.9	95.8
Outside subpopulation	N/a	N/a	95.1	94.8	96.9	97.9	96.9
No. associate taxa	12	14	25	15	25	28	18
Associate taxa (no. m ⁻²)	0.55	0.38	0.001	6.64	1.78	1.07	0.78

3) on log transformed dependent variables. Population and transect were considered fixed effects in the ANOVA model because of the non-random location of *M. vimineum* populations across the landscape (John 2002). Plants along transects were considered independent because of the randomized procedure we used to locate each one. We also assessed treatment effects on reproductive allocation (RA), which was calculated as seed biomass/total plant biomass × 100% (Gibson 2002). Because of the unbalanced design, a Type III Sum of Squares was used (Shaw and Mitchell-Olds 1993). Only one plant survived on transect D at CH, thus these data were excluded from analysis. Soils data were analyzed using a 1-way ANOVA with population as the treatment. The Tukey-Kramer all pairs test was used to compare means for significant treatment effects. Matched pairs t-test was used to compare overhead canopy cover during Fall 2000 and Spring 2001 inside and outside the subpopulations at DS. A Principal Components Analysis on the correlation matrix of the morphological variables was used to obtain an integrated measure of plant performance. Significance of axes using PCA was tested using Parallel Analysis (Franklin et al. 1995). The first component scores for each plant were analyzed for population, transect nested within population, and date factors using the same ANOVA model as for the individual morphological measurements. The seed bank and seed dispersal data were not analyzed statistically because the preponderance of zero values in these data from collections made outside the subpopulations would render analysis invalid. All statistical

analyses were conducted using SAS Version 8.0 and JMP Version 4.0.4 (SAS Institute Inc 1999).

Results. DIXON SPRINGS STATE PARK 1999. The seven *M. vimineum* subpopulations at DS ranged in size from 2.3 to 16,706 m² with *M. vimineum* cover ranging from 35 to 100% (Table 1). All subpopulations occurred under a forest canopy of > 80% cover. Overhead canopy cover immediately outside the subpopulations was similar to the canopy cover directly over (inside) the subpopulations (matched pairs t-tests; Fall 2000, $t = 1.19$, $df = 4$; Spring 2001, $t = 1.05$, $df = 5$, for both tests $P > 0.05$).

Fifty-eight vascular plant taxa were observed co-occurring in or at the margin of the *M. vimineum* subpopulations in Fall, 1999. The number of taxa per subpopulation ranged from 12 to 28 (Table 1). There was not a statistically significant relationship between subpopulation size and the number of taxa (Spearman Rho = 0.23, $P = 0.61$). Invasive species co-occurring with *M. vimineum* included *Lonicera japonica*, *Lespedeza cuneata* (Dum.-Cours.) G. Don. and *Rosa multiflora* Thunb.

Microstegium vimineum plants at DS in the flowering subpopulation were larger than the non-flowering plants in all characters measured (Table 2). The most substantial difference was in total biomass; flowering plants were almost eight times larger than non-flowering plants. The flowering plants were 1.7–4.0 times larger than non-flowering plants for all other characters analyzed.

Flowering plants had a mean of 9.5 inflorescences on 70 mostly cleistogamous spikelets.

Table 2. Morphology of *Microstegium vimineum* plants (mean \pm 1 se) at Dixon Springs State Park collected inside and outside the flowering subpopulation ($n = 20$ plants per subpopulation). A 1-way ANOVA tested the effect of subpopulation type (inside versus outside) on log transformed values of plant growth. The test was not performed when all values in one subpopulation type were zero (n/a).

Character (number per plant except where specified otherwise)	Inside	Outside	$F_{1,39}$	P
Leaves				
Functional	28.6 \pm 4.4	13.8 \pm 1.7	15.26	0.0004
Total	56.7 \pm 7.3	20.3 \pm 2.6	34.98	<0.0001
Nodes				
Total	44.9 \pm 4.5	16.2 \pm 1.4	66.63	<0.0001
Aboveground	42.1 \pm 4.5	14.9 \pm 1.3	64.58	<0.0001
Rooting nodes	6.0 \pm 0.7	3.6 \pm 0.4	4.87	0.03
Tillers				
Prop roots	5.7 \pm 0.9	1.9 \pm 0.3	18.68	0.0001
Inflorescences	5.1 \pm 0.7	2.0 \pm 0.3	8.31	0.006
Cleistogamous inflorescences (%)	9.5 \pm 2.8	0	n/a	
Dispersed inflorescences	62	0	n/a	
Spikelets	0.5 \pm 0.2	0	n/a	
Seeds	65.9 \pm 18.5	0	n/a	
Viable seed	2.8 \pm 1.6	0	n/a	
Total length (cm)	0.71	0	n/a	
Biomass (g)	150.4 \pm 22.8	37.6 \pm 5.1	68.38	<0.0001
Seed & spikelets	0.03 \pm 0.01	0	n/a	
Seed	0.003 \pm 0.002	0	n/a	
Total plant	1.6 \pm 0.21	0.20 \pm 0.04	75.67	<0.0001

Seed production was low with only 2.8 (\pm 1.6, with 0.73 \pm 0.71 viable) seed per plant. Very few inflorescences had released their seed. Reproductive allocation estimated as the biomass of seed divided by total plant biomass, was 0.19%.

Seed traps placed inside ($n = 10$) and outside ($n = 24$) *M. vimineum* subpopulations captured seed only in the three traps that were placed inside subpopulation 3. Overall, 104 \pm 78.6 seeds m^{-2} were being dispersed and were reaching the soil surface in this subpopulation. Of these, 34.8 \pm 24.6 seeds m^{-2} (33%) were viable. Across the whole *M. vimineum* population, seed rain was 10.2 \pm 7.5 viable seeds m^{-2} ($n = 34$ seed traps).

No seedlings of *M. vimineum* emerged from the seed bank samples collected prior to flowering in Fall 1999, or from samples collected outside the *M. vimineum* subpopulations. Forty-three (\pm 14.7) seedlings m^{-2} emerged from upper soil horizon (0–5 cm depth) samples collected within subpopulations in Spring, 2000. An order of magnitude fewer seedlings (4.6 \pm 3.0 m^{-2}) emerged from samples collected from deeper soil (5–10 cm depth) within subpopulations.

Seedling emergence in the field in Spring 2000 varied widely (range 0.0–23.9 seedlings m^{-2}) among the 7 subpopulations with a mean

of 5.5 \pm 2.1 seedlings m^{-2} . The highest density of seedlings emerged within the area of the flowering subpopulation from 1999. Outside of the subpopulations, seedlings were only observed adjacent to subpopulation 4 (1.6 seedlings m^{-2}), suggesting limited spread of the population in 2000.

COMPARISON AMONG FOUR POPULATIONS: 2000. Throughout the growing season, marked plants increased in the numbers of tillers, leaves and in total plant length (Fig. 1, abc). Plants at BS, CH, and LC showed a dieback between days 294 (October 21) and 321 (Nov 17), whereas plants at DS had still not started to senesce by the date of the last observation even though they were in seed. The individuals at DS were the largest, while those at CH grew the slowest, and remained the smallest (Table 3). Although smaller, the plants at CH produced similar amounts of seed per individual as the large plants at DS. Consequently, the RA of the CH plants was substantially larger than that of plants in other populations.

Survivorship of marked plants differed among populations (Fig. 1d). The population at DS, which was monitored throughout the season, exhibited a constant rate of mortality with just over 50% (23 of 50) of the marked plants surviving

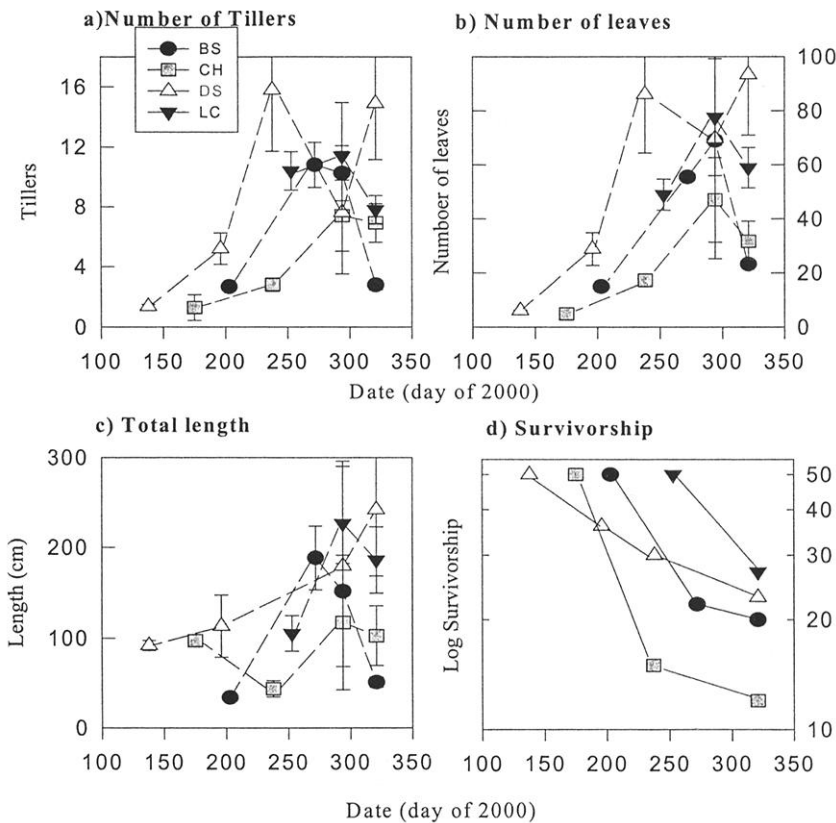


Fig. 1. Growth (a,b, & c) and survivorship (d) of *Microstegium vimineum* at four populations in southern Illinois during 2000. Means \pm one standard error are given for growth.

until day 321. By contrast, although marked at different times, the other three populations each showed an initial high rate of mortality. At CH, mortality was highest, with only 30% (12 of 50) of the marked plants surviving until day 321. The cause of mortality varied among individuals. At DS, most plants appeared to die due to herbivory (stems were browsed/clipped to ground level). At CH, all of the plants on at least one transect were washed away by floodwater, whereas of the 10 plants along a second transect, 5 individuals were dead, one was missing, two survived only as a stem, and one was found uprooted and lying on an adjacent rock on day 237. At BS, all 10 plants on one transect were destroyed by vandalism.

Plants collected on days 294 (2 plants per transect) and day 321 (remaining plants) exhibited a high correlation among the 8 morphological variables (Spearman's Rank correlation $r = 0.46-0.91$, $n = 103-115$, $P < 0.0001$ for all comparisons). Of the surviving plants, 103 of 115 (90%) produced an inflorescence (no sig-

nificant difference among populations, $\chi^2 = 1.91$, NS at 3 df).

ANOVA on the measurements for days 294 and 321 indicated significant population, transect, date, and population-by-date interactions for all of the variables measured (Table 3). Population-by-date interactions were significant for 8 of 10 variables. This trend can be seen clearly in terms of numbers of tillers and leaves of plants from BS (Fig. 1 a,b,c), and also occurred for the number of nodes, spikelets (Fig. 2) and other reproductive characters (inflorescences, seed, RA).

Number of spikelets per plant served as a useful and representative measure of overall plant performance (Spearman's $R = 0.63-0.89$, $P < 0.0001$, $n = 114$ plants for 8 morphological variables). There were 81.7 ± 14.6 spikelets per plant, ranging from 0 to 1192. The frequency distribution of spikelet production was markedly left-skewed (skewness = 4.5) with 34 of 114 plants producing 10 or few spikelets. Spikelet number varied significantly among all popula-

Table 3. Characteristics of *Microstegium vimineum* plants and soils among four populations in southern Illinois in 2000. BS, Bell Smith Springs, n = 28; CH, Cove Hollow, n = 19; DS, Dixon Springs, n = 31; LC, Lusk Creek, n = 37 (36 for seed biomass and RA). F-values from ANOVA on final measurements. Dependent variables represent counts unless indicated otherwise. RA = reproductive allocation. All variables were log transformed prior to analysis. * P < 0.05, ** P < 0.01, *** P < 0.001. Error df = 92, except seed characters where df = 91. PCA axis 1 df = 90. Population df = 3, transect nested in population df = 13, date df = 1, population*date df = 3. Soil analysis based upon 5 samples per population, one per transect, except DS where samples were analyzed from the seven subpopulations from 1999 and the four additional transects from 2000. Population means in a row sharing the same letter are not significantly different at P = 0.05 (all pairs Tukey-Kramer test). Analysis of pH calculated after back transforming to H⁺ ion concentration.

Trait	BS	CH	DS	LC	Population	Transect nested in Population	Date	Population by Date
Length (cm)	79.8 ± 12.7	107.9 ± 33.1	228.8 ± 61.0	197.0 ± 32.3	5.04**	6.95***	2.10	2.07
Tillers	4.9 ± 0.8	7.1 ± 1.2	13.0 ± 3.0	8.7 ± 1.18	1.74	5.99**	2.62	7.95**
Nodes	34.6 ± 4.4	28.6 ± 4.4	66.0 ± 13.6	54.7 ± 7.4	2.56	3.23**	0.09	3.30**
Leaves	36.3 ± 5.6	37.3 ± 7.4	87.2 ± 19.9	63.9 ± 7.9	3.28**	4.83***	6.10**	5.05**
Inflorescences	5.1 ± 1.4	9.1 ± 2.74	30.9 ± 9.4	16.7 ± 2.4	6.78**	6.05**	24.32***	9.73***
Spikelets	36.3 ± 12.3	71.3 ± 39.1	98.1 ± 40.1	105.2 ± 19.1	7.96***	4.24***	43.78***	5.90**
Seeds	2.3 ± 1.0	42.3 ± 26.3	48.1 ± 16.0	16.2 ± 3.1	12.39***	2.97**	11.98***	2.81*
Seed Biomass (g)	0.003 ± 0.001	0.17 ± 0.16	0.04 ± 0.01	0.02 ± 0.003	2.54	1.19	3.44*	4.88**
Plant Biomass (g)	0.5 ± 0.8	0.3 ± 0.1	1.2 ± 0.3	1.2 ± 0.2	6.40**	6.07***	2.56	1.45
RA	0.4 ± 0.2	51.6 ± 45.5	6.1 ± 1.6	2.8 ± 0.6	3.89*	0.90	6.06*	5.17**
PCA Axis 1	-0.54 ± 0.14	-0.26 ± 0.16	0.24 ± 0.24	0.33 ± 0.13	4.02**	5.92***	4.68*	4.31**
pH	5.4 ^B	5.1 ^{AB}	4.6 ^A	4.6 ^{AB}	4.16*			
P (µg g ⁻¹)	5.8 ± 0.5 ^B	13.0 ± 1.5 ^A	6.7 ± 0.8 ^B	6.6 ± 0.1 ^{AB}	8.54***			
K (µg g ⁻¹)	82.0 ± 11.1 ^{AB}	72.0 ± 4.3 ^B	116.8 ± 10.8 ^A	36.6 ± 3.7 ^B	10.94***			
Ca (µg g ⁻¹)	961 ± 221 ^A	643 ± 146 ^{AB}	424 ± 51 ^B	300 ± 67 ^B	6.47**			
Mg (µg g ⁻¹)	133.4 ± 18.7 ^{AB}	114.8 ± 9.1 ^B	205.7 ± 22.9 ^A	55.2 ± 4.2 ^B	9.45***			
CEC (meq 100 g ⁻¹)	5.8 ± 0.8 ^{AB}	5.4 ± 0.4 ^{AB}	7.4 ± 0.6 ^A	3.6 ± 0.8 ^B	6.25**			
Organic matter (%)	1.8 ± 0.3	1.2 ± 0.1	1.5 ± 0.1	1.5 ± 0.3	1.52 ^{NS}			

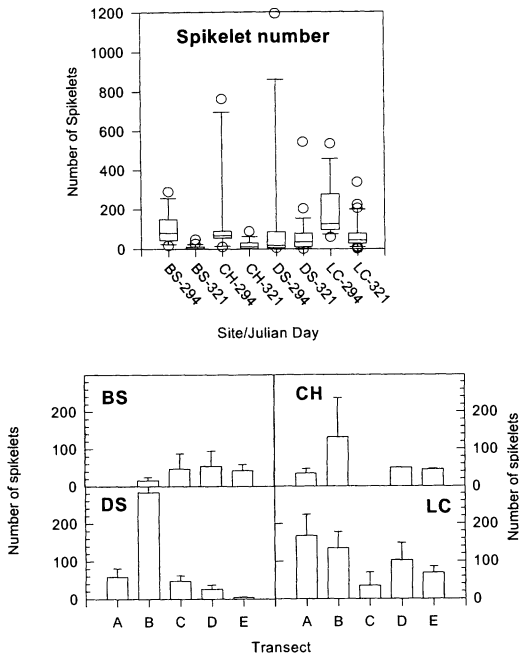


Fig. 2. Number of spikelets on *Microstegium vimineum* plants from four populations in southern Illinois during 2000. Upper panel: among populations on two sample dates (box-plot showing the median (central line), 25th and 75th percentiles, 90th percentile (upper bar), and individual values beyond the 90th percentile). Lower panels: among transects and within populations (mean plus 1 se bar). BS = Bell Smith Springs, CH = Cove Hollow, DS = Dixon Springs, and LC = Lusk Creek.

tions, interacting with transect number and date (Table 3; Fig. 2). Spikelet production was most variable at DS where the largest number of spikelets were produced on plants along Transect B located in a shady ravine. The flowering subpopulation from 1999 (Subpopulation 3 of 1999, transect A in 2000) also produced a relatively large number of spikelets. Plants at LC were less variable than those at DS (Fig. 2), and produced a larger number of spikelets per plant.

A Principal Components Analysis of 112 plants for which a complete set of 10 morphological measurements were available yielded a single significant component. All the morphological variables had large positive loadings (> 0.695) indicating that plants assigned high factor loadings had large values for all the variables. The scores from this first axis thus provide an integrated measure of plant performance. This component accounted for 74% of the variation in the data (Eigenvalue = 6.67) and was significantly related to the interaction between population and date ($F_{3,90} \text{ date*population} = 4.31, P$

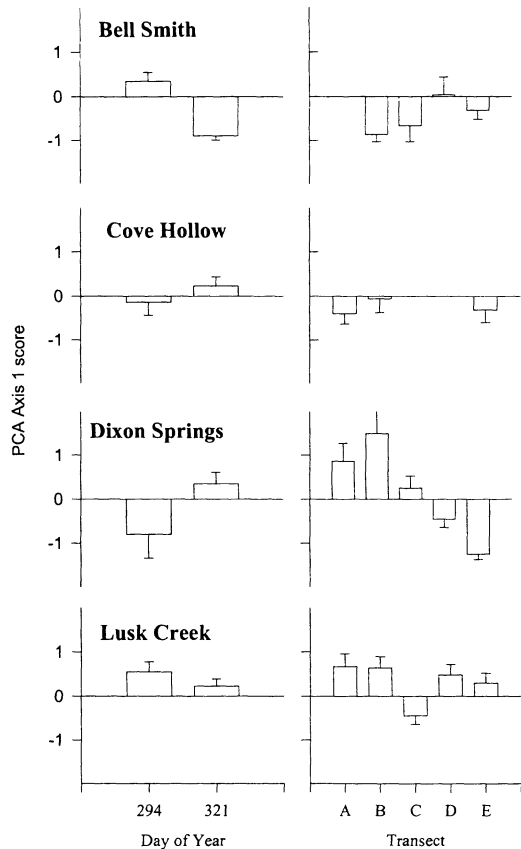


Fig. 3. Principal Component Axis 1 scores for *Microstegium vimineum* plants from four populations in southern Illinois sampled on days 294 and 321 (left panels), and along five transects (right panels).

= 0.0069; Table 3). A plot of the mean first axis scores by population and date reinforces the view obtained from separate analyses of each morphological variable (Fig. 3). Large axis 1 scores indicate that the plants at LC on day 294 were larger than those from all other populations on day 294, and remained larger than those from two of the other three populations on day 321. BS plants were also relatively large, but became the smallest group of plants by day 321. The plants at DS were the smallest of all the plants on day 294, but were the largest plants on day 321. The CH plants were also small on day 294, and increased in size only slightly by day 321. Significant variation in size occurred among transects within populations ($F_{13,90} = 5.92, P < 0.0001$) reflecting within habitat variation. This was clearly illustrated with the plants at DS which spanned the range of PCA axis 1 scores (Fig. 3). Plants on transect A and B were larger relative to those on transects D and E.

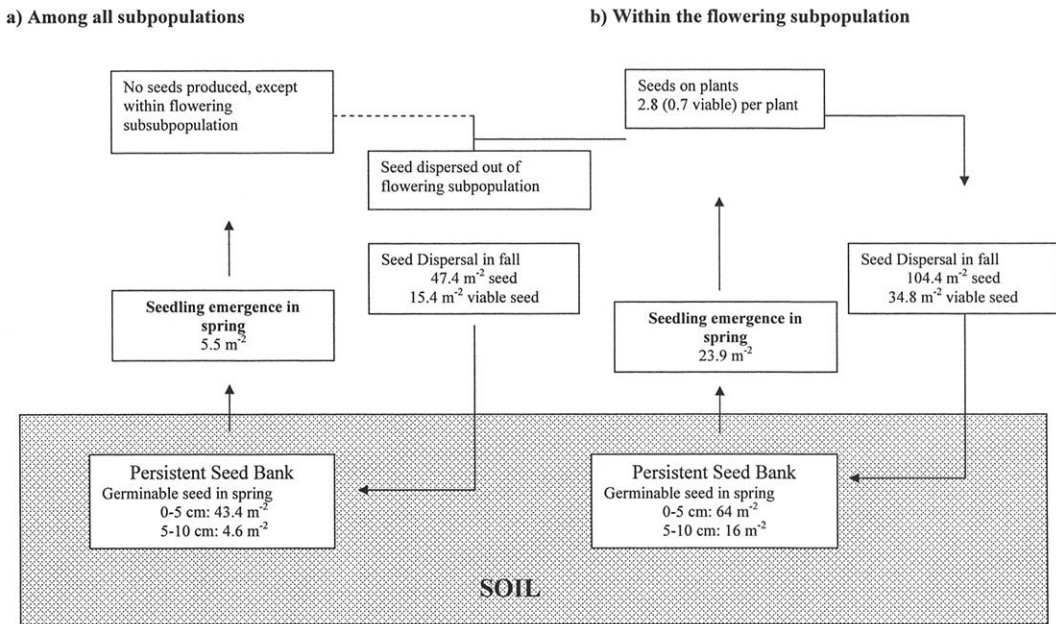


Fig. 4. Schematic model illustrating seed dynamics of *Microstegium vimineum* at Dixon Springs State Park, 1999–2000, a) among all populations, b) within the flowering subpopulation.

Soils among the four populations were generally sandy or silty loams, with low amounts of clay (data not presented). The streamside soils from the BS and LC populations were noticeably high in sand (55–85% at BS, 64–87% at LC). There were significant differences in soil pH and exchangeable cations among the populations (Table 3). The soils from DS were acidic, had the highest CEC, and contained the highest levels of K, and Mg. Calcium levels were highest at BS, whereas soil P was highest at CH. Percentage organic matter was low, ranging 0.9–2.8% and did not differ among populations.

Mean plant performance per transect (i.e., PCA axis 1 score, Fig. 3) was negatively related to the % silt and CEC of the soil (Spearman Rank Correlations, $R = -0.67, -0.55$, $P = 0.02$ for both, $DF = 17, 12$, respectively), and was positively related to % sand ($R = 0.69$, $DF = 12$, $P = 0.01$). Plant performance showed a trend towards a negative relationship with overhead tree canopy cover ($R = -0.61$, $DF = 9$, $P = 0.08$).

Discussion. A simple, schematic model summarizing seed dynamics of *M. vimineum* was developed based on our observations of seed production, seed dispersal, seed bank germination, and seedling emergence from DS (Fig. 4). This model provides a context for the interpretation

of our results from DS in 1999 and 2000, and the other three sites sampled in 2000. Data on potential seed losses to herbivory or pathogens are unavailable, and have not been reported for *M. vimineum*, but may reduce some of the estimates (Crawley 1988). Nevertheless, the model illustrates our current understanding of seed production and dispersal, and seedling emergence dynamics of *M. vimineum*.

VARIATION IN PERFORMANCE. Our study demonstrates significant variation in performance of *M. vimineum* within and among populations. This variation in performance confirms experimental studies (Winter et al. 1992; Horton and Neufeld 1998; Williams 1998; Claridge and Franklin in press) indicating that *M. vimineum* shows a plastic response to varying habitat conditions. Variation in performance in our study was primarily correlated with soil and overhead canopy cover. Extreme environmental events such as stream flooding can eliminate populations, e.g., floodwater at CH. Conversely, temporal variation can override spatial variation as we observed seed production reduced to a single, small, restricted subset of the population in 1999 (see below). Similar findings were made for *Bromus tectorum*, another invasive, annual grass (Mack and Pyke 1983).

Performance of *M. vimineum* improved with

decreasing availability of soil cations (negative relationship with cation exchange capacity) decreased soil silt content and overhead canopy cover, and increased soil sand content. The relationship with overhead tree canopy cover is consistent with observations of Winter et al. (1992) who showed that *M. vimineum* is shade-tolerant, but thrives at moderate light levels. Performance of *M. vimineum* is limited in nutrient stressed environments (Claridge and Franklin in press), but the light environment appears to be more frequently limiting (Barden 1987; Winter et al. 1992; Horton and Neufeld 1998). Soils in our study were acidic, sandy or silty loams with low levels of organic matter. Kourtev et al. (1998) found soils with these characteristics to be typical of *M. vimineum* dominated plots in hardwood forests of New Jersey. They suggested a feed-back between the presence of this exotic plant and the soil mediated by the presence of earthworms. In addition, *M. vimineum* is reported to promote positive feedback processes with the soil (decreasing litter decomposition and immobilizing N) enhancing its ability to spread (Ehrenfeld et al. 2001).

REPRODUCTION, DISPERSAL AND ESTABLISHMENT. *M. vimineum* is reported to flower prolifically and to produce large numbers of viable seed (Williams 1998). Nevertheless, despite the high abundance of *M. vimineum* at DS, plants in only one location survived to flower and set seed in 1999. The plants that did flower were larger in all morphological features measured compared to those that did not. In addition, 62% of the flowers on these plants were cleistogamous indicating a high level of self-pollination (Campbell et al. 1983). This small group of fecund plants that flowered in 1999 produced similar-sized plants in 2000 (e.g., 69.5 ± 18.5 and 59.2 ± 22.5 spikelets per plant in 1999 and 2000, respectively). In drought years such as 1999, this high light, trailside location likely acts as a seed source, which in addition to the seed bank, replenishes surrounding sinks. Accordingly, flowering was widespread throughout the *M. vimineum* population at DS in 2000, but the most vigorous plants occurred in a different area compared with the largest plants in 1999 (ie. transect A, with 283.6 ± 143.0 spikelets per plant).

Our observation of poor flowering of the DS population in 1999 indicates that high fecundity does not always occur in this species. Flowering in populations of *M. vimineum* appears to be susceptible to late season drought. The southern

Illinois region suffered a drought in July–September 1999 and received only 13% of the normal precipitation (National Weather Center records from Paducah, KY). Thus, soil moisture status may be as or more important than light and soil nutrients for invasion of this species (Horton and Neufeld 1998; Williams 1998; Claridge and Franklin in press). Although *M. vimineum* is shade-tolerant (Winter et al. 1992; Horton and Neufeld 1998), our data supports the assertion that flowering is restricted in times of moisture stress to high light microhabitats.

Our data support anecdotal accounts (Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997) and experimental observations in the field (Barden 1987) which suggests that *M. vimineum* possesses a persistent seed bank (Fig 4). However, Williams (1998) presented conflicting evidence from laboratory tests which showed 23–95% of seed germinated within 30 days of collection. We only observed seedlings of *M. vimineum* in late Spring suggesting that seed dispersed in the Fall are dormant, and overwinter prior to germination. Furthermore, significant numbers of seedlings emerged from subpopulations in Spring 2000 that did not possess adult flowering plants or receive dispersed seed in 1999. The density of emergents from the spring samples ($43.4 \pm 14.7 \text{ m}^{-2}$) was greater than the seed rain the preceding Fall ($15.8 \pm 11.5 \text{ m}^{-2}$ viable seed in traps inside subpopulations: Fig. 4) indicating carry-over from earlier years. Soil collected prior to flowering did not contain germinable seed suggesting an annual dormancy/nondormancy cycle in which seed failing to germinate in the Spring become dormant again (Baskin and Baskin 1998). The longevity of the seed bank for *M. vimineum* would likely be mitigated through mortality of seed death from pathogens or predation (Crawley 1992). Indeed, observations by Barden (1987) suggest a maximum longevity in the soil of 3 years for *M. vimineum* seed.

The viable seed rain density was almost three times the seedling emergence density ($15.8 \pm 11.5 \text{ m}^{-2}$ versus $5.5 \pm 2.1 \text{ m}^{-2}$ among all populations; Fig. 4) indicating that there was little depletion of the seed bank despite the drought and low seed set in 1999. *M. vimineum* was extirpated following the drought year in only one of the subpopulations. Persistence of the entire *M. vimineum* population at DS occurred despite the lack of flowering and seed production at all subpopulations except a very small portion of subpopulation 3. The plants in this flowering

subpopulation were large, but an extremely thick layer of thatch (litter from last year's senesced plants) in the spring may have limited seedling emergence in 2000 (Molofsky et al. 2000). A thick layer of thatch may act as an intraspecific negative feedback as anecdotal accounts suggest that attempts at *M. vimineum* control with prescribed fire at DS increases recruitment (personal communication, Jody Shimp).

M. vimineum can reestablish itself at high density even following a poor seed year given a persistent seed bank. The widespread flowering and seed set in 2000 likely served to recharge the seed bank across all existing populations. This pattern is in contrast to some other exotic annual grasses, such as *Bromus tectorum* which does not possess a persistent seed bank but is wholly dependent upon annual seed production and dispersal for population persistence (Mack and Pyke 1983).

Previous studies suggest that disturbance, such as flooding or mowing, favors establishment of *M. vimineum* and it is usually found along stream courses and riparian corridors (Barden 1987). The streambed at LC provides adequate soil moisture and allows establishment, but the scouring and frequent flooding appear to limit survivorship and performance. Consistent with some other annuals (e.g. *Vulpia fasciculata* Watkinson 1997), highest mortality of *M. vimineum* was early in the season (Fig. 1) and only 40–50% of individuals survived to flowering. Nevertheless, even seemingly established plants, such as the mid-season plants marked at LC, were susceptible to mortality in highly disturbed streambeds.

M. vimineum will continue to persist at DS, even though flowering and seed production are temporally and spatially susceptible. The presence of the soil seed bank means that new populations of *M. vimineum* can reestablish annually. Repeated annual efforts must be made to prevent flowering and seed set. We concur with others that the best strategy for controlling *M. vimineum* is removal of the plant by hand or mechanical means late in the growing season before seed production and after seed set of most co-associates (Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997; Virginia Natural Heritage Program)

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