Invasion of Microstegium vimineum (Poaceae), An Exotic, Annual, Shade-Tolerant, C_4 Grass, into a North Carolina Floodplain

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ABSTRACT: *Microstegium vimineum,* an Asian annual C_4 grass that is very shade-tolerant, has invaded floodplains, streambanks and adjacent mesic slopes in the North Carolina Piedmont during the past 30 years. A 3-year study of its invasive characteristics revealed that *M. vimineum* is slow to invade undisturbed vegetation, but rapidly fills disturbed, mesic, shaded areas, such as streamsides where floods scour existing vegetation or sewer-line rights-of-way which are mown once a year. Its seeds remain viable for at least 3 years in the soil seedbank and rapidly germinate to produce a new cohort if a disturbance removes an existing cohort. On fertile floodplain sites, soil fertilization in March had no effect on seed production in October. When *M. vimineum* seeds were sown into existing vegetation, seed production was negatively correlated with soil potassium, calcium, silt and *p*H, probably because the more fertile sites also supported a denser ground vegetation layer. These qualities, in addition to its cleistogamous or apomictic reproduction, help explain how *M. vimineum* has spread throughout the eastern U.S. since its introduction approximately 70 years ago.

INTRODUCTION

Microstegium vimineum (Trin.) A. Camus is an annual grass species from Asia which recently invaded floodplains, streamsides and adjacent mesic slopes in the North Carolina Piedmont. It appears to be advancing into the existing ground cover of floodplains, which consists mainly of Japanese honeysuckle *Lonicera japonica* Thunberg. These two species often occur in dense monospecific stands which are separated by a strikingly narrow zone of mixing. This pattern of an introduced annual grass invading established stands of Japanese honeysuckle, a perennial woody vine which is known for its aggressiveness on fertile sites of the Carolinas (Bruner and Shearin, 1964), led me to ask the following questions: (1) Is *M. vimineum* invading undisturbed stands of *L. japonica*? (2) Does *M. vimineum* create a seedbank? (3) Can *M. vimineum* invade undisturbed stands of *L. japonica* if its seeds are sown in the stands in large numbers? (4) What environmental variables are related to success of *M. vimineum* sown in stands of *L. japonica*? (5) Does *M. vimineum* respond to an increase in essential soil elements with greater reproductive success? (6) Does *M. vimineum* alter the soil so as to inhibit growth of *L. japonica*? (7) What is the role of disturbance in the invasion of *M. vimineum*?

Microstegium vimineum is in the tribe Andropogonae, subfamily Panicoideae. It was first collected in the United States in 1919 near Knoxville, Tennessee (Fairbrothers and Gray, 1972). By 1933 it had been collected in the mountains of western North Carolina (Blomquist, 1948; Fairbrothers and Gray, 1972) and by 1964 in 35 counties in North Carolina, primarily in the Piedmont (Radford *et al.,* 1968). By 1972 the species had spread to at least 14 eastern states, from Florida to New Jersey and W to Ohio and Mississippi (Fairbrothers and Gray, 1972), and by 1978 to Arkansas (Smith, 1978). In Asia the species occurs in Japan, Korea, China, Ryukyus, Formosa, Malaysia, India and the Caucasus (Ohwi, 1984).

Microstegium vimineum is unusual in that it is a C_4 plant which, unlike typical C_4 plants, is adapted to low light conditions (Brown, 1977, Winter *et al.,* 1982). Under netting which transmitted 18% full sunlight, dry matter production was not significantly reduced from production in full sunlight; at 5% full sunlight, growth was 17% of that at full sunlight (Winter *et al.,* 1982). Apparently, the C_4 pathway itself has no inherent disadvantages, compared to the C_3 pathway, under conditions of low light (Pearcy, 1983; Pearcy and Troughton, 1975).

Both cleistogamy and chasmogamy have been reported for *Microstegium vimineum* in Japan, with all flowers on axillary racemes cleistogamous (Tanaka, 1975). Near Charlotte, N.C., anthers are rarely seen extending from flowers and then only in ca. 10% of the racemes of plants grown where moisture and light are abundant. I have never observed anthers extending from flowers of plants grown in heavy shade, nor have I observed stigmas extending from flowers on any plants (Barden, pers. observ.).

The study area was a floodplain with a forest of *Acer negundo* L., *Fraxinus pennsylvanica* Marshall and *Platanus occidentalis* L. located on the Ecological Reserve on the campus of the University of North Carolina at Charlotte. Ground vegetation was primarily *Lonicera japonica* and *Microstegium vimineum.* In summer, light beneath the canopy ranged from 3-12% full sunlight; in April before leaf emergence in the canopy, light on the forest floor was ca. 40% full sunlight. At the study area, *M. vimineum* begins germinating in March, reaches 5-10 cm in height by the time of canopy leaf emergence in April, flowers in September and sheds its seeds in October.

The alluvial soil of the study area was primarily sandy clay loam or sandy loam, with a relatively high cation exchange capacity of 14.8 ± 0.4 meq/100 g ($\pm$SE), base saturation of $82 \pm 1\%$ and *p*H of 5.2 ± 0.06 on 40 experimental plots. Soil moisture (% dry weight) was $38 \pm 2.0\%$ 1 week after heavy rain and $23 \pm 1.5\%$ after 4 rainless weeks on 20 plots in the floodplain.

METHODS

Experiment 1.—To check for natural invasion by *Microstegium vimineum* into undisturbed stands of *Lonicera japonica,* 10 line intercepts, each 5 m long, were placed throughout the study area in June 1982 across sharp interfaces between adjacent stands of *M. vimineum* and *L. japonica.* In July, 1983, 10 more intercepts were similarly established. The vegetation along the intercepts was not disturbed and cover of each species was measured to the nearest 10 cm when the lines were established and at the end of the experiment in 1985. Measurements in 1985 were made within 10 calendar days of initial measurements to minimize differences in phenological development between years. Change in cover of *M. vimineum* on the 20 lines was statistically analyzed by paired t-test in which final cover was paired with initial cover.

Experiment 2.—A seedbank experiment was begun in 1983 to determine how long *Microstegium vimineum* seeds survived in the soil. An isolated 2-m^2 stand of *M. vimineum* on an upland site 100 m from the floodplain was chosen for study because floods could not transport new seeds into it and because of the absence of *Lonicera japonica* or other potential competitors on the site. A similar stand 25 m from the first was chosen in 1984 for a second seedbank test. The two stands of *M. vimineum,* which were along a footpath used daily during another study in 1977-1981, probably originated from seeds accidentally transported from the floodplain on clothing. Each year before seeds were produced, all plants in the two populations were counted and removed from the sites. Care was taken not to transport any new seeds into the seedbank sites.

Experiment 3.—Twenty lines, each 5 m long, were established in undisturbed *Lonicera japonica* stands which contained no *Microstegium vimineum* before the experiment. The first and last 1-m section of each line was sown with 3 g of *M. vimineum* seeds (approximately 2400 seeds $\cdot m^{-1}$) in October 1982. The center section of each 5-m line was left unsown, as a control. The experiment was designed to determine whether *M. vimineum* could establish self-perpetuating populations in undisturbed stands of *L. japonica. Microstegium vimineum* plants were counted during summers of 1983 and 1984, and seed heads were counted in October 1983 and 1984. The length of each seed spike was also measured in 1984 so that the number of seeds produced could be estimated from an allometric regression equation.

Experiment 4.—Several soil, biotic and other environmental factors were measured at each of the 40 lines where *Microstegium vimineum* seeds were sown to determine which factors might be correlated with the relative success of each population in producing seeds. The factors measured were LAI of all species, cumulative photosynthetically active radiation (PAR), litter depth, soil chemical properties (N.C. Dep. Agric. Soil Testing Service) and soil water-holding qualities (percent dry weight after 1 and 4 rainless weeks). Leaf area index (LAI) of all species on these lines was measured in late July, 1982-1985, with a point intercept frame of 10 pins, 10 cm apart (Mueller-Dombois and Ellenberg, 1974). Cumulative PAR was measured with two LICOR 190SB sensors as standards and Friend's (1961) diazo paper technique for the 40 simultaneous measurements. Light measurements were made twice, on a clear and an overcast day. Statistical analysis was by correlation of seed spike numbers against environmental variables.

Experiment 5.—To determine whether addition of essential elements to the soil would increase seed yield, nine pairs of 1 X 1 m plots were established in stands of *Microstegium vimineum*. The two plots of each pair were separated by 1 m and were matched for similarity of vegetation, microtopography and density of overhead canopy. In March 1985 one randomly chosen member of each pair was watered with 4 liters of an aqueous solution of 15-16-17 N-P-K fertilizer with seven micronutrients (Peter's Peat Lite Special, 45 g dry wt/plot). In April the lengths of the 10 longest stems in each plot were measured and compared to detect treatment effects on vegetative growth, and in October all seed spikes in two 20 X 20 cm subplots of each plot were counted to detect effects on reproductive success. Analysis of treatment effect was by two-way ANOVA with paired plots as blocks, and stems and subplots as replications.

Experiment 6.—To test whether some factor other than direct competition for space or light inhibited the growth of *Lonicera japonica* in stands of *Microstegium vimineum*, six plots, 1 X 5 m, were placed across the interface of juxtaposed stands of the two species so that one end of each plot was in a *M. vimineum* stand and the other in a *L. japonica* stand. In early June 1982 these plots were cleared of all vegetation, litter and roots to a depth of 5 cm. Twenty small *L. japonica* plants (10 cm tall), cut from end sections of extending vines in the study area, were transplanted into each plot, 25 cm apart along the 5-m center line. Rain during and after the transplanting made additional watering unnecessary. Half of the plants were placed in the area formerly occupied by *L. japonica* and the other half in the former *M. vimineum* area. The plots were weeded during 1982 and 1983 to eliminate potential competition. At the end of the experiment in late July 1983, survivorship of the transplanted *L. japonica* was noted and growth determined by measuring the total length of vines produced by each plant. Mortality data were tested for independence of treatment by contingency test, and growth data were compared with two-way ANOVA with the six plots as blocks.

Experiment 7.—During the intervals between weeding in the preceding experiment, the cleared area of the six plots was rapidly invaded by *Microstegium vimineum*. This observation prompted an experiment to document the invasion of the grass into the weeded areas. After data on mortality and growth of transplanted *Lonicera japonica* had been collected in 1983, the plots were left unweeded until June 1985, at which time cover of vegetation below 1 m was measured inside and outside of the plots with the point-intercept frame. One of the original six plots was omitted because a tree fell across it in 1984. Cover of *M. vimineum* inside and outside the two parts of the plots was analyzed by two-way ANOVA with the five plots as blocks, followed by a planned comparison (Sokal and Rohlf, 1981) of cover inside both ends vs. cover outside in the undisturbed *L. japonica* stand.

In all statistical analyses, data were tested for normality and homogeneity of variances before using parametric tests. Nonparametric tests were used where these assumptions were not met. Significance of statistical tests is indicated by the symbols ^{ns}, *, ** and ***, which indicate, respectively, not significant, $P < 0.05$, $P < 0.01$ and $P < 0.001$.

RESULTS

Experiment 1.—The test for natural invasion by *Microstegium vimineum* into undisturbed stands of *Lonicera japonica* was a simple experiment, but a flood in the 2nd year added unexpected complexity. The first 10 intercepts were established in June 1982 and were remeasured for species cover in July 1983, 20 days after a flood had inundated them with 20-60 cm of running water. As a consequence of flood damage, cover of *M. vimineum* declined from 48% in 1982 to 23% in 1983. But by 1985 *M. vimineum* had recovered and increased its cover to 55%. In July 1983, 10 new line intercepts were established. *Microstegium vimineum* cover increased on these from 42% to 51% in 2 years. For the 20 lines combined *M. vimineum* extended its cover into *L. japonica* stands at an average rate of 3 cm • $year^{-1}$ (t = 2.29*).

Experiment 2.—Despite the absence of any new seed production by the two *Microstegium vimineum* stands in the seedbank experiment, a new cohort of plants germinated each year for 3 years. The numbers of plants produced at the first seedbank site each year from 1983-1986 were ca. 1000, 256, 44 and 0, respectively. At the second site, the numbers were 857, 47 and 29 for 1984-1986. The last possible date for seed production at the first site was 1982, indicating a maximum seed longevity of 3 years in the soil. An unexpected test of *M. vimineum*'s seedbank occurred on 9 April 1982 when a controlled burn in an unrelated experiment killed a dense stand of young *M. vimineum* growing on an upland drainage area that had been clear-cut in 1981. The straw of the previous year's population, which was dry and matted on the ground, provided ample fuel for a hot ground fire which killed all of the new cohort of *M. vimineum* seedlings. However, by mid-June a second cohort had germinated and covered the site with a dense stand of grass.

Experiment 3.—Less than 1% of the *Microstegium vimineum* seeds sown into undisturbed *Lonicera japonica* stands in 1982 produced plants in 1983. By 1984, 12 of the original 40 populations were extinct, 20 others contained 20 or fewer plants, and only one population produced more than the 2400 seeds that were sown on each line in 1982. In total, the ratio of 1982 seed input to 1984 seed output was 6:1, a notable failure for a rapidly spreading weed.

Experiment 4.—Correlation of the number of seed spikes produced on 40 lines in 1983 with environmental variables indicated that reproductive effort by *Microstegium vimineum* was negatively correlated with soil *p*H (– .62**), zinc (– .51**), potassium (– .46**), percent silt (– .43**), LAI of other species (– .39*) and calcium (– .32*). Plots where *M. vimineum* had become extinct by 1984 had higher soil *p*H (median of 5.5 vs. 5.1**) and percent silt (18 vs. 10*), as well as greater cumulative PAR on an overcast day (0.72 vs. 0.57 mol $\cdot m^{-2}$ $\cdot day^{-1}$*), deeper litter (8.6 vs. 5.5 cm**) and greater LAI of other species (1.3 vs. 0.7*) than plots where populations survived (Mann-Whitney tests).

Experiment 5.—Addition of soil nutrients to treatment plots of *Microstegium vimineum* in mid-March resulted in stems that were 23% longer than stems in unfertilized plots by mid-April (F_s = 30.21**; df = 1, 162), but by late October no effect of the fertilization was detected in the number of seed spikes produced (F_s = 1.08^{ns}; df = 1, 18). Analysis of soil chemistry in September indicated increased phosphorus as the only significant effect of fertilization on soil chemical properties (F_s = 8.45*, df = 1, 8).

Experiment 6.—Mortality of *Lonicera japonica* plants transplanted into soil that had previously supported *Microstegium vimineum* was no greater than mortality of plants transplanted into soil that had supported *L. japonica* (5 vs. 7% mortality ^{ns}, Fisher Exact Test). Nor was there a difference in length of *L. japonica* vines grown in the two treatment soils (F_s = 1.34^{ns}, df = 1, 5).

Experiment 7.—When weeding was discontinued on the transplant plots of the previous experiment, *Microstegium vimineum* rapidly filled the unvegetated space despite the 1-year headstart of the transplanted *Lonicera japonica*. Two years after weeding was discontinued, *M. vimineum* comprised 63% of the LAI inside the plots for both ends combined, compared to 14% outside the plots in the undisturbed *L. japonica* stands (F_s =

41.5***, df = 1, 20). Cumulative PAR at these plots was 3-12% of the PAR of full sunlight.

Discussion

The rate of invasion of *Microstegium vimineum* into undisturbed stands of *Lonicera japonica* was influenced by at least three unpredictable weather events in addition to flooding. A record low temperature of −20 C in January 1985 killed most of the upper leaves of *L. japonica,* normally an evergreen plant, and undoubtedly reduced its photosynthate production during early spring of that year. Late frost in April of 1982, 1983 and 1985 killed 10-50% of *M. vimineum* seedlings on open unsheltered sites, with some mortality in the study area. However, late-germinating seeds and plastic growth of individual plants could easily compensate for this early mortality. Droughts during July 1983 and August-September 1984 undoubtedly slowed growth of *M. vimineum*. In contrast, 1985 was a moist year without floods during the growing season, and *M. vimineum* produced stands which were thicker and more luxuriant than in 1983 or 1984. Flooding in June of 1982 and 1983 inundated ground vegetation for several hours and left a layer of silt on leaves of ground vegetation. Several days after floodwaters subsided many of the *M. vimineum* leaves developed lesions which remained small (1-2 mm) and caused no mortality.

The observed 3 cm/year rate of invasion of *Microstegium vimineum* into undisturbed *Lonicera japonica* stands is too slow to account for the 10-30 m wide zone of *M. vimineum* along the floodplain drainage creek, assuming that the species arrived at the study site within the last 30 years and that it spread in a single front from the creek bank. Rather, *M. vimineum* must have spread by establishing satellite populations within the area of flooding on patches of soil left bare of vegetation by the floods. A very high flood occurred in November 1985 near the end of this study, corroborating this hypothesis; the area of worst flood damage to vegetation coincided with areas where *M. vimineum* is most abundant in summer. In the future, the intensity and frequency of floods in the study area will increase because of rapid urbanization which is occurring in the floodplain watershed, providing additional habitat for invasion by *Microstegium vimineum*.

The failure of experimentally sown populations of *Microstegium vimineum* to invade undisturbed stands of *Lonicera japonica* is further evidence of a requirement for some type of opening or disturbance in existing ground vegetation before new populations can become well-established. Supporting evidence for this view was observed near the study area where annual mowing of a 5-m-wide sewer line right-of-way has fostered the growth of one of the densest and tallest stands of *M. vimineum* observed in 3 years. In the mountains of North Carolina, stands are frequently seen along shaded, damp roadsides that are mown once or twice a year, but these populations have not spread into the undisturbed forest beside the road.

The negative correlations between reproductive success and soil *p*H, zinc, potassium, base saturation, percent silt, calcium and LAI of other species suggest that on fertile floodplain sites *Microstegium vimineum* is not limited directly by soil fertility, but indirectly by its inability to invade existing ground vegetation. Indeed, the sites of the 12 extinct populations in the seeding experiment had not only higher soil *p*H and calcium content, but also greater LAI of other species of ground vegetation, more light and deeper litter than the sites where *M. vimineum* survived. The failure of soil fertilization to increase reproductive effort was further evidence of the unimportance of soil nutrients in the distribution and abundance of *M. vimineum* in floodplain forests. The lack of evidence of allelopathic effect of *M. vimineum* on *Lonicera japonica* and the slow rate of invasion of the grass into undisturbed ground vegetation, along with observations of its rapid invasion into disturbed sites, indicate that *M. vimineum* is a successful weed which is able to spread more rapidly than *L. japonica* into shaded, mesic, disturbed sites.

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