FACTORS AFFECTING GROWTH AND REPRODUCTION IN THE INVASIVE GRASS *MICROSTEGIUM VIMINEUM*

A Thesis

by

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Submitted to the Graduate School

Appalachian State University

In partial fulfillment of the requirements for the degree of

Master of Science

May 1998

Major Department: Biology

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ABSTRACT

FACTORS AFFECTING GROWTH AND REPRODUCTION

IN THE INVASIVE GRASS *MICROSTEGIUM VIMINEUM*

(May 1998)

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Microstegium vimineum, an invasive grass from Japan and elsewhere in Asia, has become a common pest in forest understories throughout the eastern U.S. Its presence is of particular concern in areas such as Great Smoky Mountains National Park, where it forms dense stands, displacing native plants. The focus of this study was to determine environmental requirements for growth and reproduction in this invasive grass. Field measurements were made of sunlight, soil moisture and presence of other species, as well as stand level growth and plant level growth, flowering strategy, and seed production of *M. vimineum*. Individual plant growth increased linearly with increasing sunlight, while stand level growth peaked between 30% and 40% sunlight, decreasing slightly at higher light levels. Low soil moisture and competition with other plants in sunny sites appear to limit *M. vimineum* to forest understories. Stand density was inversely related to percent sunlight and ranged from 100 to over 3,000 plants/m^2. Plant characters such as number of culms and plant height decreased with increasing density, suggesting that

individual growth was constrained by intraspecific competition. Most plants created cleistogamous flowers, but larger plants were more likely to produce chasmogamous flowers. Flower type was not correlated with sunlight or soil moisture, however, disturbed habitats produced proportionally more chasmogamous flowers. Number of seeds per plant was positively correlated with plant biomass, culm length, and number of leaves. Estimated seed production ranged from 16,000 to 50,000 seeds/m^2. On the basis of previous field studies, *M. vimineum* was reported to create a seedbank that lasted 3-5 years. However, in the laboratory all viable seeds germinated, even in the dark, suggesting that dormancy is neither innate nor dark-induced. It may be that the dormancy mechanism was inhibited by the laboratory procedures used. Further study is needed to clarify whether *M. vimineum* creates a true seedbank.

M. vimineum's growth form and reproductive strategy give it the potential to colonize new habitats and then persist indefinitely. Because of its high fecundity and dispersal potential, it is likely to continue to spread in the United States. Control of established stands has proven difficult. Land managers concerned about the invasion of *M. vimineum* should concentrate control efforts in wet, sunny sites where seed production reaches its maximum.

ACKNOWLEDGMENTS

Thanks go to Drs. Howard Neufeld, Robert Creed, and Gary Walker, and to Mr. Keith Langdon, all of whom served on my thesis committee. Thanks also go to my numerous field and greenhouse assistants: Kristi Adcock, Andy Baldwin, Leigh Bass, Carol Benner, Michelle Brown, Kevin Lapp, Todd Leaven, Sean Thorpe, Simms Toomey, Jennifer Robertson, and Jerald Weaver. Betsy Cobb, Betsy Harris, and Dr. Wayne Van Devender provided help and materials. Dr. Mitch Cruzan provided the fisheye camera lens and computer resources for hemispherical photography. Special thanks go to my roommate and friend Alice Adams for her patience, support, and willingness to listen.

Funding was provided by Sigma Xi, Cratis D. Williams Graduate School, and ASU Graduate Student Association Senate.

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INTRODUCTION

Biological Invasions

The flux of species between geographic regions is a phenomenon that has occurred throughout evolutionary time. Taxa may speciate in geographic isolation, then cross dispersal barriers through natural or artificial events and colonize new habitats (Brown and Gibson 1983). The natural rate of invasions is fairly low, but in the twentieth century there has been an unprecedented escalation in the rate of biological invasions due to increasing migration and movement of materials by humans (Elton 1958). This recent increase in biological invasions is a significant but poorly recognized constituent of global change (Vitousek et al. 1996). Invasive species, freed from their natural predators, pathogens and competitors, are often able to rapidly colonize new habitats and outcompete native species (Crawley 1987, Blossey and Notzold 1995).

Biological invasions have wide-ranging economic, social, and ecological consequences. A well-documented example is the invasion of the Eurasian zebra mussel (*Dreissena polymorpha*) into lakes and waterways in North America. The mussels have built up in such numbers that they have reduced water flow into industrial intake pipes. Cleanup is expected to cost $3.1 billion dollars over ten years (Office of Technology Assessment 1993). Even more devastating is the potential risk posed by the invasion of the Asian tiger mosquito (*Aedes albopictus)* which made its way into the U.S. in used

automobile tires imported for resale. The mosquito is a vector for yellow fever, dengue fever and equine encephalitis, all of which can be fatal to humans (Craven et al. 1988).

But the ecological consequences of biological invasions may be more severe than the economic and social consequences. Invasions have caused extinction of native species through competition, predation, herbivory and hybridization; higher incidences of diseases and disease vectors in native species; and changes in ecosystem properties such as productivity, nutrient cycling and disturbance (see Simberloff, 1990, Vitousek et al. 1996). Invasions have homogenized ecological communities and resulted in an overall loss of biological diversity on a global scale (Soule 1990). Invasive species are found on every continent and every remote island on earth. In fact, islands have been the hardest hit by the impacts of exotic organisms (e.g., Vitousek et al. 1987). On the island of Guam, for example, the brown tree snake (*Boiga irregularis*) has caused the extinction of nine of the eleven native forest birds and has left the island almost devoid of all native birds (Savidge 1987). Exotic plants comprise as much as 50% of the total plant species in some islands, and as much as 20% in some continental countries (Vitousek et al. 1996).

Invasive species are also a problem in national parks and refuges (Usher et al. 1988, Houston and Schreiner 1995). In Great Smoky Mountains National Park (GSMNP), there are 1,656 total species of vascular plants, of which 370 are exotic (Keith Langdon, pers. comm.). Most of these plants are remnants of ornamentals left by residents displaced by the Park Service and are not considered a threat to natural communities. But a minority of these plants are aggressively invading new habitats

within the park and causing severe impacts to park ecosystems (Clebsch and Wofford 1989).

Most invasions have been poorly documented and their effects are often not well known. However, it is clear that exotic species can increase rates of extinction (Simberloff 1990). A number of studies have documented that exotic species reduce the habitat available to native species through direct competition for growing space, soil or light, frequently causing further risk to native rare and endangered species. *Melaleuca quinquenervia*, a tree native to Australia, has displaced hundreds of thousands of acres of cypress in south Florida (Myers 1984). Several species of honeysuckle, including *Lonicera tatarica, Lonicera japonica* and *Lonicera mackii,* have become major pests in the eastern U.S., forming dense stands in forest understories, displacing native herbaceous plants and tree seedlings (Woods 1993, Luken and Thieret 1996).

Invasive species can exert a strong influence over ecosystem processes such as energy flow, nutrient cycling, water availability and disturbance patterns (Vitousek 1986, Vitousek 1990, D'Antonio and Vitousek 1992). But ecosystem level effects can be difficult to assess and additions of species in a community may or may not have measurable effects on the entire system. Invading plants that differ in life form, effect on soil properties, resource requirements, photosynthetic pathway, or phenology from native species can dramatically alter the properties of the ecosystems they invade. For example, two nitrogen fixing exotic plants, *Melinis minutiflora* and *Myrica faya,* have invaded nutrient poor volcanic slopes in Hawaii and changed resource availability in this habitat. These plants have made atmospheric nitrogen accessible to non-nitrogen fixing plants,

causing increased competition in what previously were sparsely populated areas, and pushing out endemic species adapted to low soil nutrient conditions (Mueller-Dombois and Whiteaker 1990, Asner and Beatty 1996). To make matters worse, most of the new colonizers are also exotics.

Feral pigs (*Sus scrofa*) are another good example of an exotic species that has changed system level resource availability. Pigs have been intentionally introduced into many areas of the world as a food source or for sport hunting. Several studies have shown that pig rooting accelerates decomposition and loss of nutrients (e.g., Spatz and Mueller-Dombois 1972, Bratton 1974, Singer et al. 1984). By mixing the top layer of litter, rooting aerates the decaying material, thereby increasing respiration and decomposition. The nutrients contained in the litter are released more quickly than the forest can take them up and end up leaching out of the system. Pig rooting also destroys herbaceous plants and the fine roots of trees which take up nutrients, further compounding erosion and nutrient leaching.

Another way that an invasive species can alter ecosystem level processes is through alteration of disturbance regimes. Many invasive grasses are highly flammable and promote fires. Some of these species have increased fire frequency in their new habitats, often preventing succession and eliminating some of the slower growing lifeforms. In South America, several grasses including *Hyparrhenia rufa*, *Melinis minutiflora*, *Panicum maxima* and *Brachiara* spp. were introduced to support cattle grazing on recently cleared forest. All of these grasses increase fire frequency and intensity, and even though large scale grazing has been reduced, the fires that these

grasses perpetuate have prevented succession back to forest (D'Antonio and Vitousek 1992).

Because exotics can create such problems, it is important to determine the conditions that control the spread of exotic species. More baseline data are needed on the ecology of many of these plants to maximize the effectiveness of control measures. Many federal land managers have programs to monitor and combat biological invasions, but often do not have the ecological information necessary to effectively combat these species. In GSMNP, a three year program to eliminate exotic plants did not include some of the most problematic species because no known form of control was both cost effective and compliant with NPS regulations and goals (Keith Langdon, pers. comm.). One of these plants was *Microstegium vimineum* (Trin.). In terms of area covered, this grass is the most problematic exotic plant in GSMNP, covering 48% of the 154 hectares listed as invaded by exotics in a 1988-1989 survey (Clebsch and Wofford 1989). This same study listed *M. vimineum* as rapidly expanding and severely impacting park environments, yet little is known about the basic ecology of this plant. The research described in this thesis developed from GSMNP's need to have better baseline data for *M. vimineum* in hopes of being able to understand how this plant spreads, what new environments it might spread to, and perhaps to better understand how control measures might be made more effective.

Biology of *Microstegium vimineum* (Trin.) - A Literature Review

M. vimineum (Trin.) is a C_4 grass native to southeast Asia. It is common in the Japanese provinces of Hokkaido, Honshu, Shikoku, and Kyushu (Ohwi 1984), and in the countries of Korea, China, Taiwan, Malaysia, India, Sri Lanka, Nepal and Pakistan (Goel and Uniyal 1983, Bor 1960, Kuoh and Chiang 1991). It reaches a maximum length of about 1 - 1.5 meters and roots frequently from the lower nodes, forming dense, clonal stands (Radford et al. 1964, Ohwi 1984). Despite deceptively weak stems and root systems, this grass quickly spreads into new habitats and excludes other species (Barden 1987). *M. vimineum* is unusual among the successful exotic grasses in that it is tolerant of deep shade and annual. Most exotic grasses tend to be shade-intolerant and perennial (D'Antonio and Vitousek 1992).

The major habitat types invaded by this species in the U.S. are river banks, flood plains, damp fields, swamps, lawns, mesic woodlands, roadside ditches, trails, utility rights-of-way, emergent wetlands, and early successional fields (Fairbrothers and Gray 1972, Hunt and Zaremba 1992, Redman 1995). First recorded in the U.S. in Knoxville, TN in 1919, *M. vimineum* had invaded all of the southeastern states by 1960 (Fairbrothers and Gray 1972), moved west to Arkansas and Texas by 1978 (Smith 1978, Nixon et al. 1987), and northward to New York and Connecticut by 1987 (Hunt and Zaremba 1992). The full extent of its current range, however, is not well known. It has become a well-established pest in the southeast and is becoming increasingly common in riparian areas of the Mid-Atlantic states (Redman 1995).

M. vimineum is capable of forming large, monospecific stands in forest understories. Its ability to form dense stands does not appear to be due to any allelopathic potential, as Woods (1989) showed that radish seeds still germinated with a leaf infusion of *M. vimineum*. Both insect and vertebrate herbivores avoid feeding on it (Keith Langdon, pers. comm.), giving it a major competitive advantage over native understory plants.

Barden (1987) found that *M. vimineum* could invade an existing stand of *Lonicera japonica* only very slowly even when the seeds were sown in very high numbers. He surmised from records of sites where *M. vimineum* has invaded that it must require a disturbance to establish a foothold in a new environment and that it may then spread by establishing satellite populations whenever new disturbances occur. Invasions of many exotic species have been correlated to ecosystem disturbance (Huenneke et al. 1990, D'Antonio 1993, McIntyre and Lavorel 1994, Kitayama and Mueller-Dombois 1995, Pyle 1995). Disturbance probably accelerates invasions simply through the clearing of space which increases availability of sites for establishment and decreases interspecific competition.

Broad spectrum herbicides are the most effective form of control for this grass (Woods 1989), but due to the sensitive nature of the habitats it invades such as riparian zones, chemical herbicides are often not appropriate. In GSMNP, the application of Borax to the soil has been found to be effective, but has not been implemented as a strategy for control because its saltiness attracts deer which then disturb the soil and prevent establishment of native plants (Soehn and Johnson 1994). The same study found

that excessive nitrification, phosphorylation, and acidification of the soil; and addition of rhododendron chips were ineffective in killing the plants or preventing seed production. Burning and flooding have also been found to be ineffective in killing the seeds and mowing only serves to remove competing plants without killing *M. vimineum* (Barden 1991).

Field studies attempting to document the habitat requirements for *M. vimineum* have resulted in conflicting data. Hunt and Zaremba (1992) suggested that *M. vimineum* is cold-intolerant since its rate of northward spread has been much slower than its rate of spread in the south. Barden (1987) noted that extreme winter cold (-20° C) or late frosts could kill seedlings, however, new seeds germinated after these extreme periods, allowing the species to persist in these sites. Hunt and Zaremba (1992) found populations in New York, Connecticut and New Jersey growing only on red shale soils, whereas Redman (1995) found populations in Maryland growing on loamy soils. Also, since *M. vimineum* is a C_4 plant, it should be more efficient at utilizing soil water and nutrients than the mostly C_3 conspecifics that grow in shaded mesic areas (Brown 1978). However, site observations suggest that *M. vimineum* does not grow in xeric or drought-prone areas and Barden (1987) found a negative correlation between reproductive success and soil pH, zinc, potassium, base saturation, percent silt, and calcium. These data suggest that *M. vimineum* is not limited by soil fertility.

Plants with the C_4 photosynthetic pathway generally require high levels of sunlight. However Winter et al. (1992) found no significant difference in biomass accumulation in *M. vimineum* grown in light levels of 100%, 63% and 18% full sunlight.

Plants grown in 5% sunlight still accumulated some biomass, while other C_4 species were unable to grow at all in this low light. They also found that shade-grown plants had a 2-fold decrease in leaf thickness, a reduction in fresh and dry weight, a reduction in soluble protein, and an increase in chlorophyll content per unit leaf area over sun grown plants. These results indicate that *M. vimineum* has become especially adapted for low light environments.

Horton (1996) studied *M. vimineum's* physiological responses to light flecks. He showed that *M. vimineum* has a very low light compensation point (13 $\mu mol\ m^{-2}\ s^{-1}$), allowing the plants to effectively utilize very low levels of sunlight such as those found in heavily shaded understories. In addition, he found that *M. vimineum* has a high light saturation point (700-800 $\mu mol\ m^{-2}\ s^{-1}$) and a rapid induction rate (3.5 to 5 minutes to reach 50% of maximum photosynthesis) which enable it to take advantage of the brief, but high intensity, sunflecks that appear in forest environments. Barden (1996) showed that biomass was linearly related to light intensity in *M. vimineum* grown in high densities in pots, suggesting that it should show maximal growth in full sun situations. However, in contrast to expectations from the pot studies cited above, *M. vimineum* is almost never found in fully open sites and is most frequently found in completely closed-canopy forests.

In addition to the lack of definitive data on *M. vimineum's* environmental tolerances, very little is known about the reproductive strategy of this species. Under optimal conditions, each plant can produce as many as 1000 seeds on both terminal and axillary inflorescences (Barden 1987). It is not known how these seeds are dispersed,

though it has been suggested that some seed migration takes place in waterways (Woods 1989) and in transported hay or soil (Barden 1991). By removing germinating plant material and staking down seed nets to prevent immigration, Barden (1987) and Woods (1989) demonstrated that seeds may lie dormant in the soil for 3-5 years or more, forming an extensive seedbank.

M. vimineum produces both cleistogamous flowers (flowers that are closed and self-pollinating) and chasmogamous flowers (flowers that open and can cross-pollinate). In *M. vimineum*, cleistogamous (CL) inflorescences remain enclosed in the leaf sheath and the sheath physically prevents the florets from opening and traps the seeds, preventing their dispersal. The chasmogamous (CH) inflorescences are exserted above the sheath and when the florets open, the anthers protrude, reducing the chance of self-pollination. Because cross-pollination relies on a chance event, CH flowers are usually less often pollinated than CL flowers (Gara and Muenchow 1990). Tanaka (1975) followed 605 spikelets of *M. vimineum* in Japan and found that 97% of the CL spikelets set fruit, while only 63% of the CH spikelets set fruit.

Environmental factors influence the ratio of CL to CH flowers for many species (Waller 1980, Clay 1982, Wilken 1982, Bell and Quinn 1987, Le Corff 1993). These studies have generally shown that CL flowers predominate in stressful environments where conditions for outcrossing are unlikely. CH flowers can then still provide populations the chance to outcross when conditions are favorable. More importantly, for species such as *M. vimineum* which have sheath-enclosed CL flowers, seed dispersal is much more likely in CH flowers (Cheplick 1993). The result is that seeds from CL

flowers carry the maternal genotype and remain in the maternal environment, whereas seeds from CH flowers may carry new genotypes and can be dispersed to new environments. When considering the potential advantages of outcrossing for *M. vimineum*, however, it is important to consider that the populations in the U.S. may have come from a small founder population and there may be low genetic variability within the populations.

The research described herein focuses on determining how certain environmental factors affect growth and reproduction in the introduced grass *M. vimineum*. The objectives were to characterize the responses of *M. vimineum* to light, soil moisture, and presence of other plant species at the individual and stand levels. Specific questions to be addressed were: Why is *M. vimineum* limited to low light environments? Is *M. vimineum* drought sensitive? How do individual plants respond to environmental conditions and intraspecific competition? Is *M. vimineum*'s reproductive strategy plastic to changing environmental conditions? What percentage of the seeds are left in the seed bank the first year?

MATERIALS AND METHODS

Field Study Sites

Six study sites with extensive stands of *M. vimineum* were selected in GSMNP (Figure 1). Sites were chosen to cover the range of soil moisture and sunlight environments in which *M. vimineum* could be found. The sites were either sunny and wet, shady and wet, sunny and dry, shady and dry, or moderate in shade and soil moisture. All were flat or on negligible slopes and at elevations of 500-600 meters. Five of the sites were located within 7 km of each other in Cades Cove. The sixth site was located approximately 7 km east of Cades Cove. The proximity of the sites ensured that weather conditions were as similar as possible. All sites were evidently disturbed either before or since the Park's inception. Even the forested sites showed evidence of once having been completely cleared, as the trees appeared young and evenly aged.

Site 1. Abrams Creek Exclosure (ACX) was shady and wet. It was located within a 5+ hectare wild pig exclosure on the floodplain of Abrams Creek in the west end of Cades Cove. The herbaceous layer was thick and consisted almost exclusively of large *M. vimineum* plants. Christmas fern (*Polystichum acrostichoides*) was sparsely scattered through the site. The canopy consisted of young second growth red maple (*Acer rubrum*) and black birch (*Betula lenta*).

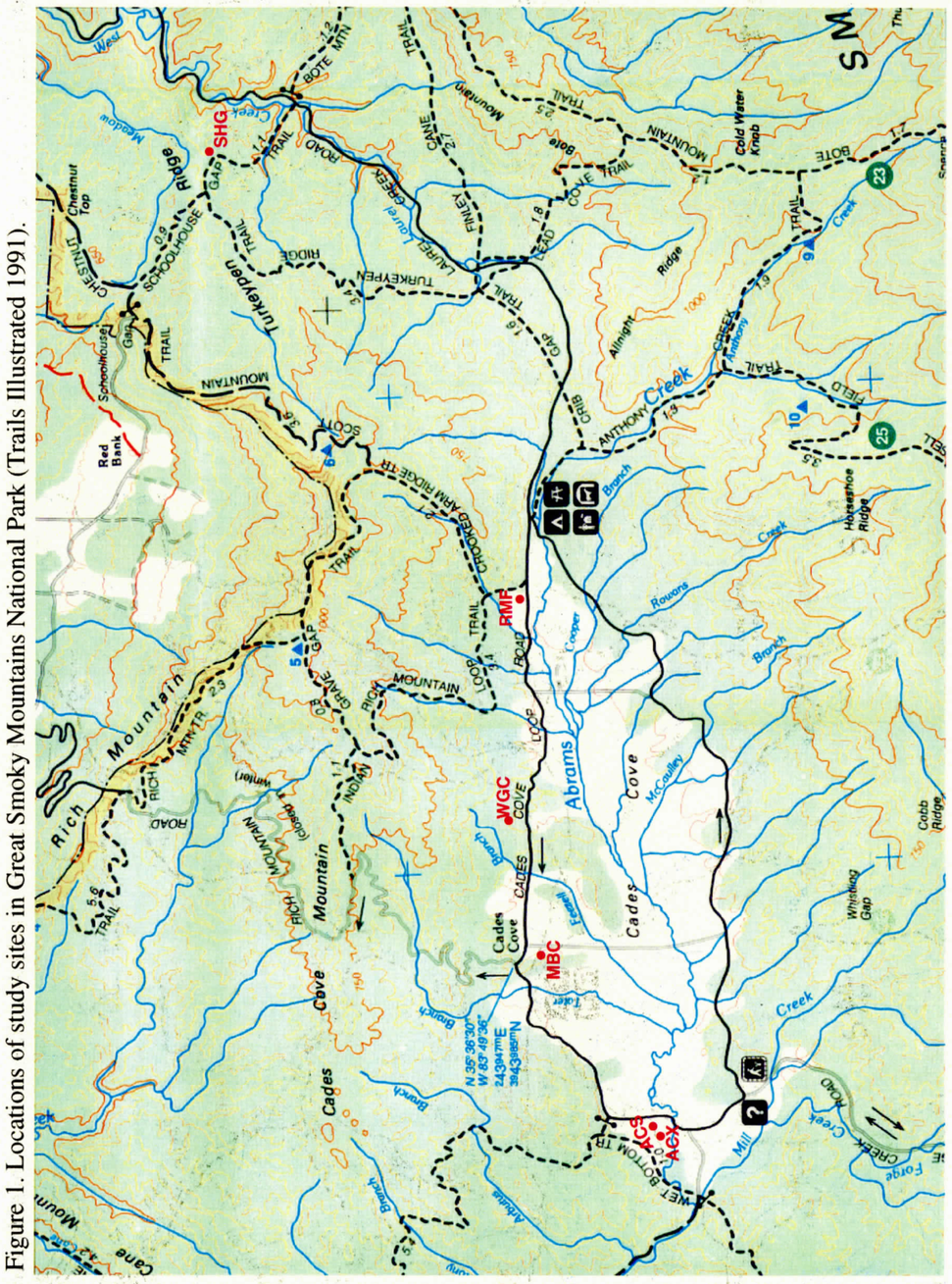


Figure 1. Locations of study sites in Great Smoky Mountains National Park (Trails Illustrated 1991).

Site 2. Abrams Creek Site (ACS) was moderately shady and wet. It was approximately 100 meters from ACX on the same damp floodplain. The soil appeared to be heavily saturated and a fine sand/gravel mix deep in the substrate may have indicated an underground seep. The canopy consisted of red maple and alder (*Alnus serrulata*), but was somewhat more open than ACX. Large individuals of *M. vimineum* formed a dense stand with some other species of grasses (Poaceae) in the herbaceous layer.

Site 3. Woods near Gregory's Cave (WGC) was shady and moderately dry. It was located in a stand of second growth tulip poplar (*Liriodendron tulipifera*) near Gregory's Cave to the north of the Cades Cove Loop Road. *M. vimineum* completely dominated the herbaceous layer and covered the forest floor, and while the plants were extremely dense, they were quite small.

Site 4. Missionary Baptist Church (MBC) was shady and dry. It was located south of the Missionary Baptist Church inside the Loop Road. The canopy consisted of tulip poplar, white oak (*Quercus alba*) and some white pine (*Pinus strobus*). The litter layer was extremely dry and consisted exclusively of *M. vimineum*. While *M. vimineum* completely covered the herbaceous layer, the plants were not as large nor as dense as in WGC.

Site 5. Rich Mountain Field (RMF) was sunny and dry. It was located along the edge of a hayfield to the north of the entrance to the Loop Road. The canopy was open to the west, placing the plants in full afternoon sun. The overhanging vegetation consisted of sourwood (*Oxydendrum arboretum*) and tulip poplar. The field is mowed at least once a year, so the study site was placed in the edge strip outside the mowed area.

This strip averaged about 3-5 m in width and was just under the treeline. There were numerous other herbaceous species mingled with *M. vimineum*, notably fescue grasses *(Festuca* spp.) that dominated the field, but *M. vimineum* dominated the edge. The individuals were very large, but by early September 1997 they had turned brown and died back probably due to lack of rain.

Site 6. Schoolhouse Gap (SHG) was sunny and wet. This was the only site not located in Cades Cove. It was in a wetland along Schoolhouse Gap Trail about 3 miles east of Cades Cove. Herbaceous plants in this wetland have suffered severe damage from hog rooting on several occasions over the past 20 years, but Park Service management has reduced the problem in recent years. This area occupied a large gap in the canopy since there were no tree species growing within the wetland. The herbaceous layer was dominated by several grasses including *M. vimineum* and *Leersia virginica*, along with jewelweed (*Impatiens capensis*), and blackberry (*Rubus* spp.). The study site was placed on the south-east side of the wetland where *M. vimineum* dominated. The plants in this site were the largest observed in GSMNP, with individuals reaching over 2 meters in length.

Field Sampling

A single line transect 12 m in length was established through the center of the stand of *M. vimineum* at each site, and rebar driven into the ground at each end for permanent marking. Quadrats 0.5 m x 0.5 m in size were located at 1 meter intervals along the transects. At SHG the transect was extended to 15m with quadrats skipped at

meters 3, 8 and 9 and the transect shifted horizontally 1 meter from meter 4 to meter 7 to accommodate for footpaths through the wetland which left the plants trampled. At each quadrat sunlight, soil moisture and aboveground plant material were measured as described below.

Field Light Measurements

Light was measured by hemispherical photography. This technique characterizes the geometry of the canopy through computer analysis of a wide-angle photograph of the sky (Rich 1989). A photograph was taken above each quadrat using a Sigma 8 mm fisheye lens and Kodak Tri-X black and white film (ASA 400) at f125 with automatic shutter speed. The camera was mounted on a tripod and leveled horizontally facing upwards, with the top of the frame oriented due north (Figure 2). The tripod was adjusted to position the camera at the top height of the herbaceous layer, so that herbaceous cover was not included in the photograph. Photographs were taken before 1000 or after 1700 local time to ensure low nadir of the sun, preventing overexposure and uneven backlighting. Photographs for SHG and WGC were taken on September 6, 1997, and those for RMF, MBC, ACX and ACS, were taken on September 7.

The film negatives were scanned into a personal computer at 512 x 512 pixel resolution and processed using Optimas 5.1 Image Analysis software (Optimas Corp., Bothell, WA). The edges of the photograph were clipped within the image to eliminate non-sky pixels from analysis and the image was rotated to adjust for declination. A threshold gray value for open sky was determined visually for each image to compensate

Figure 2. Sample hemispherical canopy photograph from ACS, taken September 7, 1997. Image analysis calculated open sky at 12.8% and open sun at 15.9%.

for different exposure levels. Percent open sky was calculated as the percent of pixels within the clipped image that appeared darker than the threshold shade of gray. To calculate direct sunlight, the portion of the sky between the path of the sun on March 31 and on October 1 was delineated from hourly solar azimuth and elevation coordinates for Knoxville, TN. These dates were used because they represent the extreme sun angles during *M. vimineum*'s growing season. Percent open sunpath was calculated as the percent of pixels that appeared darker than the threshold gray value within this range of the sky. This method of determining the position of the sun does not account for differences in light intensity among different times of the day and different seasons.

Field Soil Moisture Measurements

A 25 cm deep, 2.5 cm diameter soil core was taken at each quadrat. Two portions of the cores were used: the portion from the surface to 4 cm representing short term rainfall and conditions at the plant roots, and the portion from 21-25 cm, representing long term rainfall and soil water-holding capacity. The core samples were placed in separate film canisters and stored until they could be returned to ASU for weighing. Soil cores were taken from SHG, RMF, and WGC on September 6, 1997, and from RMF, ACS, and ACX on September 7, 1997. The soil samples were weighed to the nearest 0.01 grams on September 14, 1997, then placed in aluminum dishes and dried to a constant weight and reweighed. Percent soil moisture was calculated as:

(fresh weight - dry weight) x 100 / fresh weight

Field Plant Measurements

Aboveground biomass in 1997 was harvested from RMF on September 8, WGC on September 9, SHG on September 10, MBC on September 11, and ACS and ACX on September 12. For harvesting, a 0.5 m x 0.5 m PVC pipe frame was placed on the ground at each quadrat and all plants rooted within the frame were carefully disentangled from the plants rooted outside the frame. Plants that had main roots inside the frame but aerial roots outside the frame were counted as part of the quadrat, while plants that had main roots outside the quadrat but aerial roots inside the quadrat were removed from the sample. Stems were cut at ground level and individuals of *M. vimineum* were counted and separated from other plants. During counting, every 10th plant up to 12 plants per quadrat was measured for the length of the main culm, number of culms, number of leaves, and length and width of the 4th fully-formed leaf from the top. *M. vimineum* and other plants were placed in separate paper bags and dried to a constant weight, then weighed to the nearest 0.01 gram.

Seed production was measured on October 10 and 11, 1997 from a subsample of 20 plants from a single randomly chosen quadrat at each site. Plants were harvested at ground level as described above, and measured for length of the main culm, length of each branch, number of leaves on the main culm, number of leaves on each branch, length of each spikelet, and number of seeds on each spikelet. The spikelets were noted as being cleistogamous (CL) if no florets were visible above the sheath, chasmogamous (CH) if all florets were visible above the sheath, or intermediate (INT) if some, but not

all, florets were visible above the sheath. The plants were dried in individual paper bags at 50° C for 41 days and weighed to the nearest 0.01 gram.

Data were analyzed using Minitab 11.1 (Minitab, Inc., State College, PA). Density data were log transformed for analysis because of the multiplicative relationship between density and environmental variables. Mean plant biomass (MPB) was calculated as:

MPB = stand biomass / density

Stepwise multiple regression analysis was used to develop models of the predictive ability of measured environmental factors on stand and plant biomass, density and plant parameters. For among-site analyses, only predictors with an F-statistic greater than 4.0 were used in the model since there was a wide range of environmental conditions across sites. For within-site analyses, the ranges for variables were much narrower, so the minimum F-statistic was lowered to 1.0. Since percent open sky and percent open sun were essentially interchangeable measures of the same variable (i.e., autocorrelated), as were percent upper soil moisture and percent lower soil moisture, both variables were not used in the same model. For models that included both of either pair of predictors as significant, the lower of the two variables was removed and the model recalculated using only the higher. Plant parameters were correlated with density using linear regression analysis

Greenhouse Experiment

Seeds were collected on March 22, 1997, in Elkmont, another heavily disturbed, but more accessible, valley in GSMNP. The top few centimeters of soil were removed from an area approximately 3 m x 3 m and transported to the ASU greenhouse. The soil was mixed evenly by hand and spread over 10 soil moisture gradient boxes on March 23, 1997. The boxes were built to specifications described by Pickett and Bazzaz (1976) and were 2.44 m long x 0.61 m wide x 0.30 m deep and lined with plastic. They were inclined 0.30 m on the long end to provide flooding on one end and dry conditions on the other. Six partitions with screens at the bottom to allow water flow separated each box into soil resource states. The boxes were watered daily and fertilized biweekly with a 16-16-16 fertilizer (Southern Agricultural Inc., Boone, NC) while the seeds germinated and all plants except *M. vimineum* were removed by hand. On May 10, 1997, shadecloth simulating 92 percent shade was placed over 5 of the boxes while the other 5 were left in full sunlight. From this date on water and fertilizer were added only at the flooded end of each box and penetrated the upper compartments by flow through screens at the bottoms. Greenhouse temperature was set at 78° C for daytime and 72° C for nighttime.

On June 16-18, 1997, the plants were harvested because of overcrowding. Stems were clipped 12.7 cm from soil level and the plants from each box were separated by soil resource state. The material was dried to a constant weight in paper bags, then weighed to the nearest 0.01 g. The stems of the plants were left so that the plants could grow back and be harvested a second time. However, most of the stems died and the plants could not be reused.

Since the experiment was terminated early, no measurements were made of the actual soil moisture values within the resource states, so soil moisture effects on plant biomass were not tested statistically. Mean biomass between light treatments was compared using analysis of variance (ANOVA).

Flowering Strategy

Twelve locations in Cades Cove and eight locations in Elkmont were used to study environmental effects on flowering strategy in *M. vimineum*. Elkmont was included because there are many recently abandoned homes which have high densities of *M. vimineum* in the lawns. The 20 locations included a range of sunlight and soil moisture values and different habitat types from woods and fields to roadsides and abandoned lawns. Locations in Cades Cove were sampled on September 27, 1997, and in Elkmont on September 29, 1997. At each location, a hemispherical photograph and a soil core were taken to measure light and soil moisture using the same methodology as described earlier. Soil cores were dried at 60° C for 18 days.

Each location was additionally classified as disturbed or undisturbed. Locations were designated as disturbed if they were recently mowed or grazed by livestock. The lawns in Elkmont were designated as disturbed even though they may not have been mowed in the last several years. Undisturbed locations were exclusively within forested areas that had not undergone unnatural clearing since the inception of Park Service records for the area in 1936.

Plants in a single, randomly placed, 0.25 m x 0.25 m quadrat at each location were harvested and separated based on whether the terminal raceme was CH, CL or INT. The number of individuals of each type was counted and the length of the main culm was measured to the nearest 0.1 cm. The separated material was dried in paper bags at 50° C for 29 days and weighed to the nearest 0.01 g.

Regression analysis was used to model environmental variables as predictors of the proportion of individuals that were CH and the proportion of stand biomass of CH plants in each site. The INT flowers were grouped with the CL flowers for regression analysis because flowers with few exserted florets rarely open (Tanaka 1975). Mean plant biomass for each flower type was compared by analysis of variance. Chi square analysis was used to determine if the total number of individuals of each flower type in disturbed and undisturbed habitats was significantly different. Since mean plant biomass was higher in disturbed sites, analysis of covariance (ANCOVA) was used to determine if differences in proportion of CH individuals was higher in disturbed sites irrespective of mean plant biomass.

Seed Germination

Seeds were collected from plants at each site on October 22, 1997. Additional seeds from CL and CH plants were collected from SHG and kept separate. Seeds were removed from the sheaths and stratified in sand in a refrigerator at 5° C until January 31, 1998, when they were separated from the sand by floating in water and then placed in petri dishes lined with filter paper. Three petri dishes with 50 seeds each were used for

each site and each flower type. Each petri dish was given 3.5 mL of water and sealed with transparent tape. The petri dishes were placed in random order under a bank of four 40 watt fluorescent lights. The lights produced 35 - 55 μmol photons m^{-2} sec^{-1} as measured by a light meter (Li-Cor Inc., Lincoln, NE), and were placed on a 18-hour light, 6-hour dark schedule. The number of germinated seeds was counted every other day starting Febuary 2, 1998. On February 13, 1998, the tape was removed so that the germinated seeds could be taken out and more water added to the petri dishes. The petri dishes were resealed using plastic wrap. Germination was monitored for 30 days after which no further germination seemed likely.

On March 3, 1998, the remaining seeds were removed from the petri dishes and observed under a dissecting microscope. The palea and lemma were removed and seeds without embryos were noted, while seeds with embryos were cut in half longitudinally. One half of each embryo was soaked in a 0.1% solution of 2,3,5-triphenyl tetrazolium chloride in the dark for 2 hours to determine viability (Delouche et al. 1962). The embryos were again observed under a microscope and those that appeared red were classified as viable, while those that did not appear red were classified as not viable. Differences in final proportion of seeds germinated and seed viability among sites and between flower types were compared using analysis of variance.

On March 6, 1998, 25 seeds were placed in each of six petri dishes lined with plastic and sealed with tape. To test for light-induced dormancy, three of the petri dishes were additionally wrapped in a double layer of aluminum foil to prevent light transmission. Seeds were removed from the refrigerator, placed into the petri dishes and

sealed in about 20 minutes. The remaining three petri dishes were used as controls and were sealed and placed under lights without aluminum foil. All six petri dishes were placed under the bank of fluorescent lights for 10 days after which germinated seeds in each dish were counted. Mean percent germination was compared between treatments using analysis of variance.

RESULTS

Environmental Variation Across Study Sites

Environmental factors varied widely across study sites (Table 1). The highest value for percent open sky was only 35.8%. This was the largest percent of open sky that could be found within a stand of the required size (minimum of 12 m x 1 m) in GSMNP, and it is likely that this is the upper limit of sunlight for *M. vimineum*'s ecological range. It was difficult to find stands outside of a full canopy, and both SHG and RMF were exceptional in this respect. Most of the open sky values for ACS, ACX, MBC, and WGC were considerably below 10%.

Percent open sky and percent open sun were highly positively correlated, as were percent upper soil moisture and percent lower soil moisture (Table 2). Neither value for percent sunlight was correlated with percent upper soil moisture or lower soil moisture. When using sunlight and soil moisture data for statistical analysis of growth responses, only the variable with the higher R^2 of each pair of these values was used. Biomass of plants other than *M. vimineum* ranged from 0.0 to 335.0 g/m^2, though nearly half (32 out of 72) of the quadrats had no species present except *M. vimineum*. Those quadrats with a high biomass of other species tended to be the high sunlight sites (Figure 3A). Additionally, other species occupied a higher percentage of all plant biomass in the quadrats with high light (Figure 3B).

Table 1. Range of environmental factors and stand measurements across sites. Numbers are means, with standard errors in parentheses below. Site abbreviations are explained in the Materials and Methods chapter. N = 12 for each site.

Parameter	Combined Sites	ACS	ACX	MBC	RMF	SHG	WGC
% Open Sky	10.90 (1.34)	6.92 (0.94)	3.38 (0.35)	3.25 (0.21)	32.89 (0.64)	16.30 (0.97)	2.33 (0.14)
% Open Sun	17.96 (2.27)	9.41 (1.84)	3.43 (0.59)	5.30 (0.45)	49.88 (1.01)	36.40 (2.18)	2.60 (0.22)
% Upper Soil Moisture	28.98 (1.78)	47.24 (1.55)	46.60 (1.02)	15.06 (0.78)	10.05 (0.62)	33.59 (1.42)	23.70 (0.84)
% Lower Soil Moisture	21.83 (1.23)	29.81 (0.93)	36.58 (0.62)	11.33 (0.46)	8.46 (0.44)	27.56 (0.41)	18.14 (0.58)
Biomass of Species Other than *M. vimineum* (g/m^2)	40.36 (8.32)	7.52 (4.52)	0.00 (0.00)	0.40 (0.28)	156.36 (13.88)	73.28 (25.08)	4.16 (2.00)
% Biomass of Species Other than *M. vimineum*	12.45 (2.28)	4.50 (2.61)	0.00 (0.00)	0.47 (0.34)	45.73 (4.03)	19.17 (5.59)	4.46 (2.17)
Biomass of *M. vimineum* (g/m^2)	154.60 (9.72)	136.36 (10.12)	135.12 (7.92)	84.56 (5.08)	187.92 (17.48)	290.56 (21.92)	92.92 (5.52)
Density of *M. vimineum* (#plants/m^2)	1253.2 (94.8)	834.0 (58.4)	1442.8 (83.2)	1549.2 (111.2)	402.4 (49.2)	789.6 (69.2)	2489.2 (147.6)

Table 2. Pearson's coefficient of correlation values for percent sunlight and percent soil moisture measurements. N = 72.

Factor	% Open Sky	% Open Sunpath	% Top Soil Moisture	% Bottom Soil Moisture
% Open Sky	1.000			
% Open Sunpath	0.960*	1.000		
% Upper Soil Moisture	-0.416	-0.332	1.000	
% Lower Soil Moisture	-0.411	-0.362	0.934*	1.000

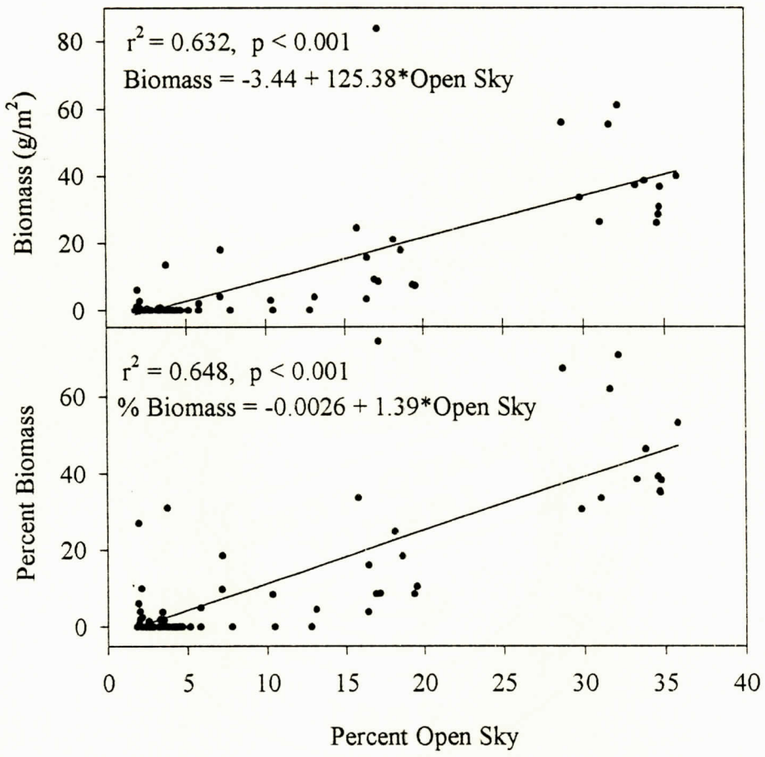
*significant at p = 0.05

Stand Level Responses to Environmental Factors

To determine stand level responses to environmental factors, multiple regression analyses were used on quadrat biomass and density. Multiple regression analysis showed that 68% of the variance in stand biomass across sites could be explained by a combination of percent open sun, upper soil moisture and biomass of plants other than *M. vimineum*, with open sun as the single most important factor (Table 3). Soil moisture was second in importance when added to the model, while biomass of plants other than *M. vimineum* also significantly improved the relationship.

Most environmental factors varied only slightly within sites, so among the 12 quadrats within each site, regression analysis revealed no significant environmental

Figure 3. Biomass (g/m2) of plants other than *M. vimineum* as (A) a function of percent open sky, and (B) as a percent of total quadrat biomass. N = 72.



predictors for stand biomass in ACX, ACS, MBC, and WGC. However, in RMF and SHG, the two highest light sites, biomass of other plants was the single best predictor of stand biomass of *M. vimineum*. Biomass of *M. vimineum* decreased significantly with increasing biomass of other species (Figure 4). Biomass of plants other than *M. vimineum*

Table 3. Results of stepwise multiple regression analysis of environmental predictors of stand biomass and density. Only predictors with an F-statistic greater than 4.0 were used. Each row shows the addition of that factor to the previous factors. Factors are listed in the order in which they were added to the model. N = 72.

Biomass (g/m^2)

Factor	Partial R^2	Model R^2	p-value
Percent open sun	0.3897	0.3897	< 0.001
Percent lower soil moisture	0.1735	0.5632	< 0.001
BOOS* (g/m^2)	0.1184	0.6816	< 0.001

Biomass = 6.59 + 128*Open sun + 73.6*Soil moisture - 0.652*BOOS

Density

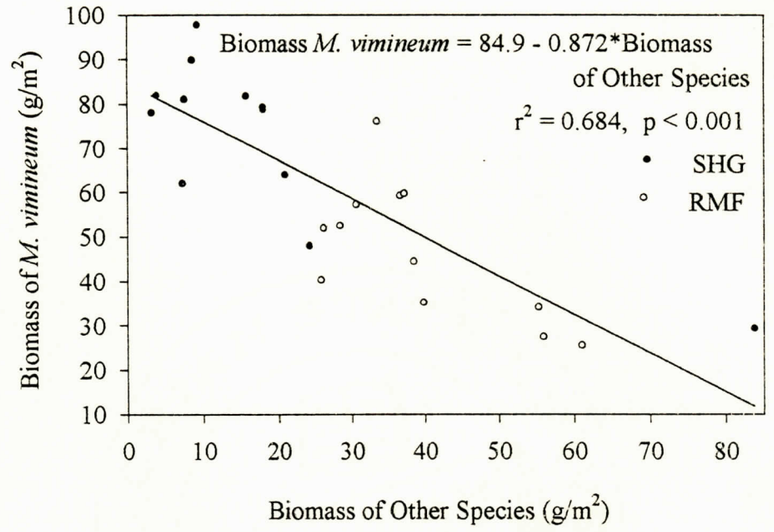
Factor	Partial R^2	Model R^2	p-value
Percent open sky	0.6306	0.6306	< 0.001
Percent upper soil moisture	0.0704	0.7010	< 0.001
BOOS* (g/m^2)	0.0413	0.7423	0.002

Log density = 2.85 - 1.80*Open sky - 0.649*Soil moisture - 0.00591*BOOS

*BOOS = Biomass of Other Species

explained 45% of the variance at RMF and 64% of the variance at SHG. Only by reducing the minimum allowable F-statistic to 1.0 did light or moisture make significant improvements to the model. For RMF, adding percent upper soil moisture improved the R^2 8.3% while percent open sky increased it an additional 10.4%. For SHG, adding percent upper soil moisture added 5.0% while percent open sky only increased it by 0.9%.

Figure 4. Stand biomass of *M. vimineum* as a function of biomass of other species in sites RMF and SHG. N = 12 for each site.



Across sites, 74% of the variance in log density was explained by a combination of factors with percent open sky again as the most important factor (Table 3). Increases in all three environmental factors caused reductions in stand density.

Plant Level Responses to Environmental Factors and Density

Plant characters were analyzed to correlate reproductive output to environmental and density-dependent factors. Table 4 shows multiple regression results for plant parameters. Percent open sun alone explained considerably more of the variance in estimated mean plant biomass than it did at the stand level, accounting for 82% of the

Table 4. Results of stepwise multiple regression analysis of environmental predictors of plant parameters. Only predictors with an F-statistic greater than 4.0 were used. Each row shows the addition of that factor to the previous factors. Factors are listed in the order to which they add to the model. N = 72.

Estimated biomass (g)

Factor	Partial R^2	Model R^2	p-value
Percent open sun	0.8159	0.8159	< 0.001
Percent top soil moisture	0.0145	0.8304	0.018

Estimated biomass = -0.0104 + 0.975*Open sun + 0.170*Soil moisture

Number of culms

Factor	Partial R^2	Model R^2	p-value
Percent open sky	0.5436	0.5436	< 0.001
Percent top soil moisture	0.0598	0.6034	0.002

Number of culms = 0.665 + 11.6*Open sky + 2.77*Soil moisture

Main culm length

Factor	Partial R^2	Model R^2	p-value
Percent open sun	0.3183	0.3183	< 0.001
Percent bottom soil moisture	0.3884	0.7067	< 0.001

Main culm length = -10.0 + 112*Open sun + 170*Soil moisture

Number of leaves

Factor	Partial R^2	Model R^2	p-value
Percent bottom soil moisture	0.3183	0.3183	< 0.001
Percent open sky	0.1095	0.4278	< 0.001

Number of leaves = 7.75 + 5.00*Soil moisture - 4.07*Open sky

variance. Soil moisture added only 1.5% to the model. Biomass of plants other than *M. vimineum* did not contribute significantly to the model. Percent open sun and percent lower soil moisture explained 71% of the variation in main culm length and 60% of the variance in number of culms, but environmental factors and biomass of other species could not explain a substantial amount of variance in other plant characters.

Density of *M. vimineum* alone explained some of the variance in number of culms, main culm length, and 4th leaf length (Table 5). Linear regression showed that density was not a significant predictor for number of leaves, and though it was significant for 4th leaf width, it only accounted for 19% of the variance. Density could not be used as a predictor of plant biomass since the values for plant biomass were derived from stand biomass and density.

Length and width of the 4th leaf were positively correlated ($r^2 = 0.814$) indicating that leaf shape is fairly stable between individuals within and across sites.

Table 5. Linear regression analysis with density as the predictor of plant parameters. N = 72.

Factor	r^2	p-value
Number of culms = 4.30 - 0.005*Density	0.429	< 0.001
Main culm length = 71.3 - 0.0766*Density	0.324	< 0.001
Number of leaves	0.029	0.156
Length of 4th leaf = 5.86 - 0.00251*Density	0.422	< 0.001
Width of 4th leaf = 0.902 - 0.00035*Density	0.193	< 0.001

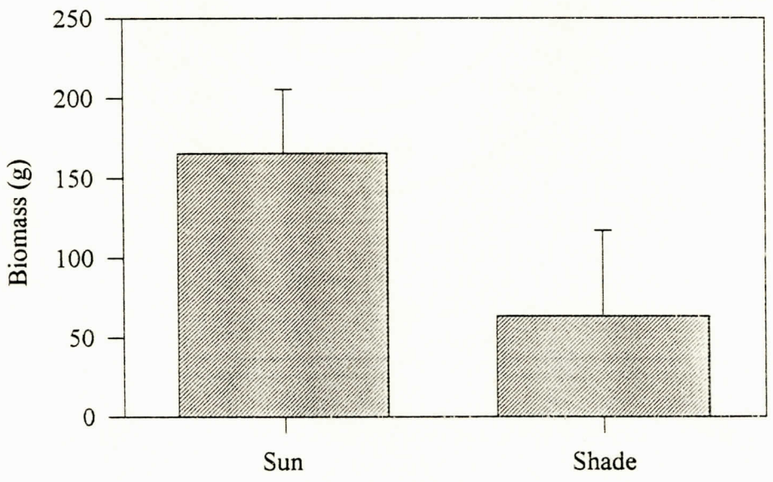
Greenhouse Experiment

Mean biomass accumulation was significantly greater (ANOVA, $p<0.05$) in the full sun treatment than in the shade treatment (Figure 5).

Flowering Strategy

Flowering strategy was analyzed for its contribution to reproductive success. Regression analysis for sunlight and soil moisture yielded no significant results for predicting the proportion of individuals with CH flowers or the proportion of the quadrat biomass for individuals with CH flowers (Table 6). However, chi-square analysis

Figure 5. Mean biomass plus standard error per soil resource state for each light treatment. N = 30.



showed a significant difference in number of CL and CH flower types between disturbed and undisturbed sites (Figure 6). The number of individuals with CH flowers was greater in disturbed sites than in undisturbed sites.

Mean biomass of plants with CH flowers was significantly greater (ANOVA, $p<0.05$) than that of plants with intermediate or CL flowers (Figure 7), regardless of environmental conditions or disturbance. Further analysis revealed that mean plant biomass was significantly greater (ANOVA, $p<0.05$) in disturbed than in undisturbed sites (Figure 8). However, analysis of covariance with biomass as the covariate showed that proportion of CH flowers was greater in disturbed sites regardless of plant biomass ANCOVA, $p<0.05$).

Table 6. Linear regression results for environmental predictors of the proportion of individuals that were CH and the proportion of biomass of CH plants. N = 20.

	Predictors	r^2	p-value
Proportion of Individuals	Percent Open Sky	0.081	0.229
	Percent Open Sun	0.090	0.077
	Soil Moisture	0.017	0.870
Proportion of Biomass	Percent Open Sky	0.083	0.219
	Percent Open Sun	0.094	0.288
	Soil Moisture	0.000	0.965

Figure 6. Number of individuals of each flower type by site disturbance history. N = 9 for undisturbed, N = 11 for disturbed. $\chi^2 = 22.13$ $p < 0.001$.

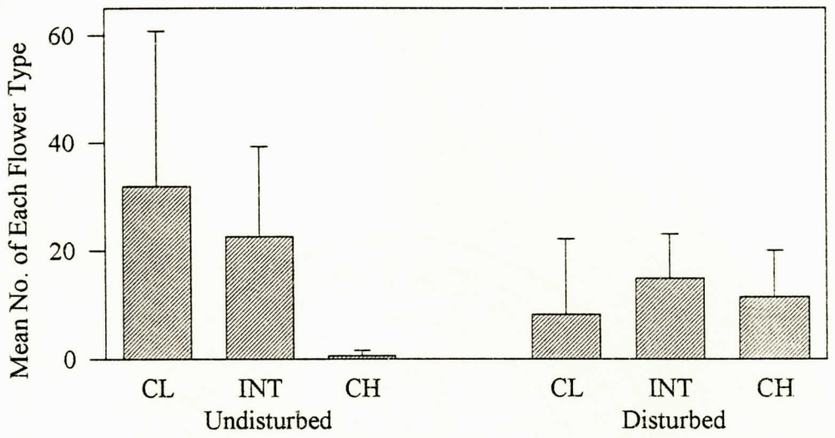


Figure 7. Estimated mean plant biomass plus standard error for individuals of each flower type. N = 16 for CL, N = 20 for INT, N = 13 for CH.

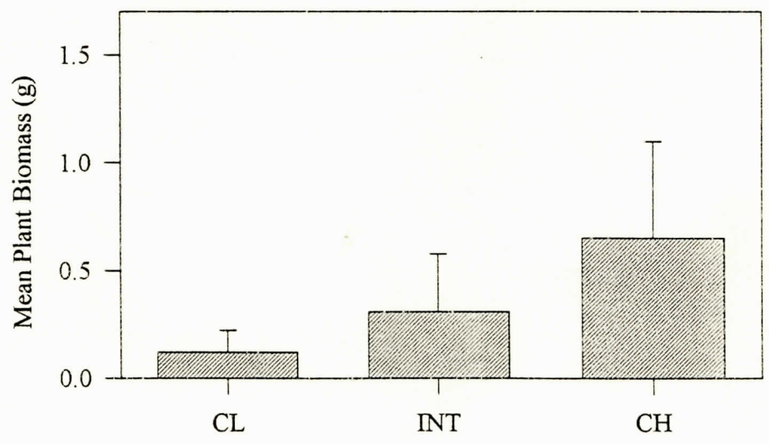
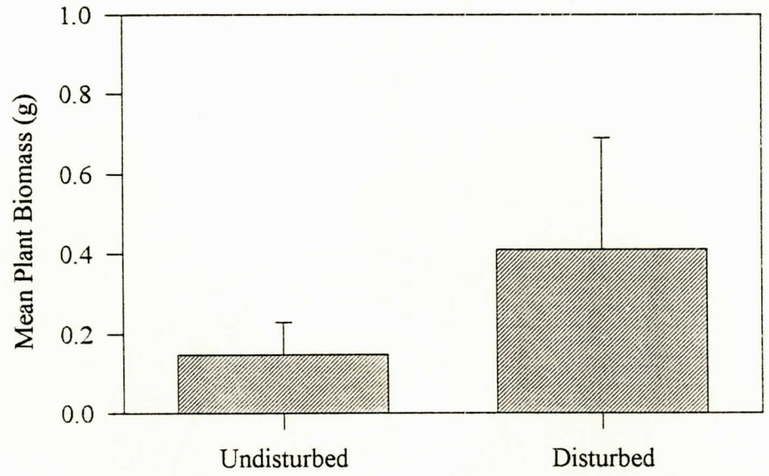


Figure 8. Mean plant biomass plus standard error by site disturbance history. N = 9 for undisturbed, N = 11 for disturbed.



Seed Production

Number of seeds per plant was strongly and positively correlated with plant biomass (Figure 9A), main culm length (Figure 9B), number of leaves (Figure 9C), and sum of culm lengths (Figure 9D). Mean number of seeds per plant varied widely within sites as a result of the large range of plant parameters. Stand level seed production was estimated from mean seed production per plant at each site times density (Table 7) and ranged from 16, 000 to 50,000 seeds/m^2.

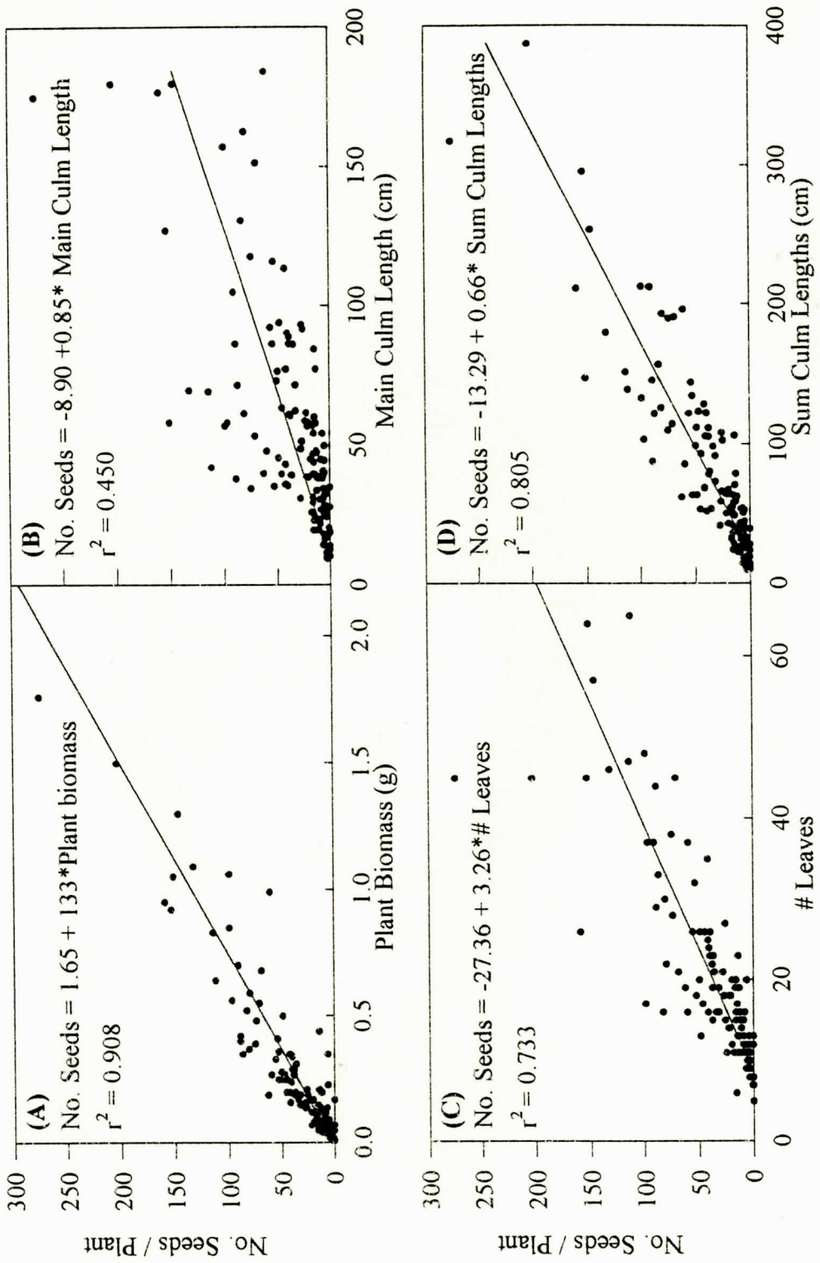


Figure 9. Seed production per plant as a function of (A) plant biomass, (B) main culm length, (C) number of leaves, and (D) sum culm lengths. N = 120.

Very few individuals within the main study sites had CH flowers, but number of seeds per plant was significantly greater (ANOVA, $p<0.001$) in individuals with CH flowers than individuals with INT and CL flowers (Figure 10).

Seed Germination and Viability

Seed germination after 30 days was greater than 90% for ACS, ACX, SHG, and WGC, 80% for MBC, and significantly less (23%) for RMF (Figure 11). Most of the ungerminated seeds did not have embryos, while the remainder were simply not viable (Table 8). No viable seeds failed to germinate in the petri dishes.

Figure 10. Seed production per plant as a function of flower type. N = 120.

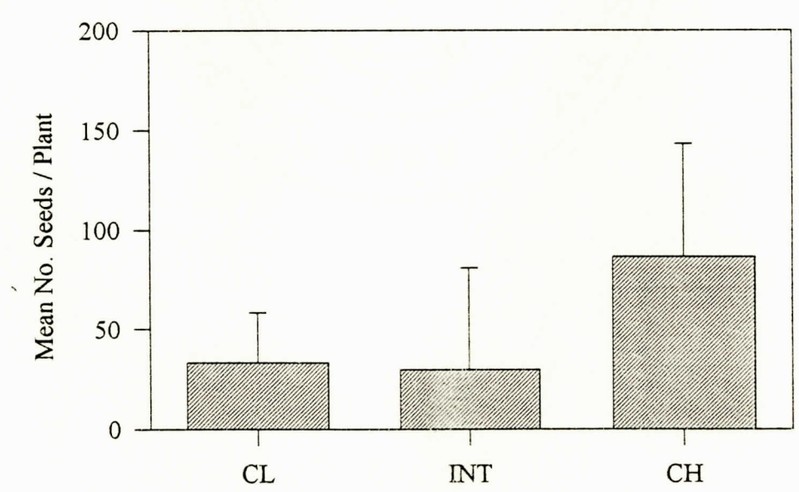


Table 7. Estimated seed production by site. N = 20.

Site	Mean no. seeds/plant ± standard error	Quadrat density	Estimated no. seeds/m^2
ACS	35.19 ± (6.42)	504	17,736
ACX	33.50 ± (6.08)	1,260	42,210
MBC	9.95 ± (1.49)	1,808	17,990
RMF	77.40 ± (15.6)	476	36,842
SHG	74.05 ± (15.9)	688	50,946
WGC	5.44 ± (0.94)	3,120	16,973

Figure 11. Germination rates for study sites. N = 3.

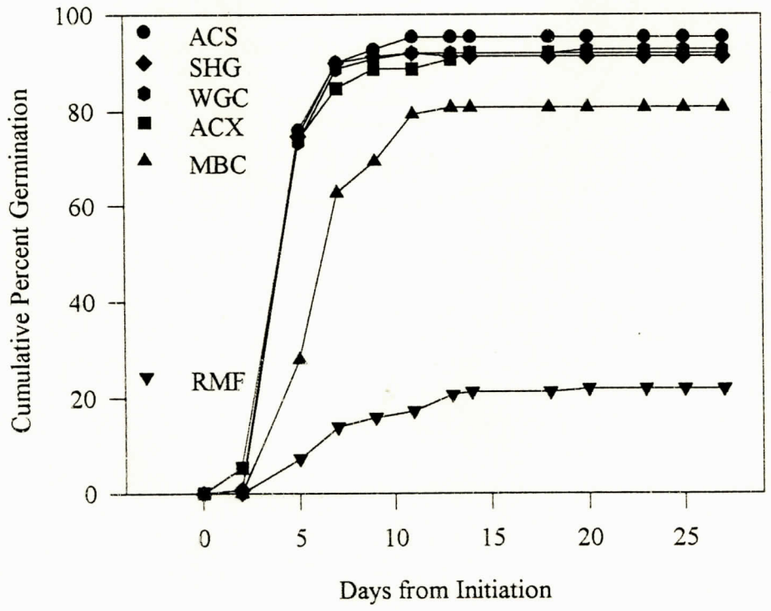


Table 8. Seed germination and viability rates for sites. Values are means ± standard errors. Means within a column followed by the same letter are not significantly different at p = 0.05. N = 3.

Site	Percent germinated	Percent without an embryo	Percent not viable
ACS	95.3 ± (1.8)a	4.7 ± (1.5)a	0.0 ± (0.0)a
ACX	92.0 ± (4.2)a	6.0 ± (3.0)a	2.0 ± (1.0)a
MBC	80.7 ± (4.4)a	18.7 ± (3.2)a	0.6 ± (0.6)a
RMF	22.7 ± (3.1)b	68.7 ± (4.6)b	8.6 ± (1.5)b
SHG	91.3 ± (2.9)a	8.0 ± (2.0)a	0.7 ± (0.6)a
WGC	92.7 ± (3.5)a	6.7 ± (2.5)a	0.6 ± (0.6)a

Germination of CH seeds was lower than the CL seeds (ANOVA, $p < 0.05$).

Again, most of the ungerminated seeds did not have embryos, and the remainder were not viable (Table 9). Seeds in petri dishes wrapped in aluminum foil still germinated, and final percent germination was not significantly different than for seeds in uncovered dishes (ANOVA, p=0.579).

Table 9. Seed germination and viability rates for flower types. Values are means ± standard errors. Means within a column followed by the same letter are not significantly different at p = 0.05. N = 3.

Flower Type	Percent germinated	Percent without an embryo	Percent not viable
CL	94.0 ± (6.0)a	4.7 ± (5.0)a	1.3 ± (1.2)a
CH	78.7 ± (4.2)b	13.3 ± (3.1)b	8.0 ± (3.5)b

DISCUSSION

Stand and Individual Level Responses to Environmental Factors

Plants tend to be very plastic in their responses to environmental conditions (Bradshaw 1965). However, restriction of a single resource may limit growth in a given environment (Tilman 1985). Alternatively, a plant may be excluded from a suitable environment if it is not able to compete with other plants given the resources available. *M. vimineum* is capable of growing in environments with light levels that are so low as to preclude growth of some species (Winter et al. 1992), yet it is not found in high light environments presumably either because soil moisture is a limiting resource or because it does not compete well in these environments.

On an individual basis, plant biomass strongly increased in close correlation with increasing sunlight, while soil moisture and presence of other species had no effect alone, and added little to the cumulative model. But variation in stand level responses tended to reflect an input of many environmental variables with sunlight as the single most important. Soil moisture may explain some of the lack of growth in full sun areas as regression analyses showed that stand biomass responded positively to increasing soil moisture. This result indicates that *M. vimineum* may be sensitive to water availability. Plants in MBC and RMF, the driest sites, appeared to be withering by the end of September when rainfall was low. Drought stress was noticeably worse in RMF, where

full afternoon sun appeared to have intensified water stress in the plants and caused them to turn brown.

SHG also received a large amount of open sunlight but had very wet soils, and while the stand biomass was high, *M. vimineum* did not dominate in the entire site. In fact, in both RMF and SHG, the two highest light sites, biomass of other species was the most important single predictor of biomass of *M. vimineum*, with biomass of *M. vimineum* decreasing as biomass of other species increased. This may indicate that *M. vimineum* is not a strong competitor in full sunlight. Horton (1996) was able to determine that *M. vimineum* had physiological mechanisms that enable it to grow in very low light, but he noted that it retains some characteristics of plants that grow in high light environments, such as a high light saturation point and rapid loss of photosynthetic induction following light reduction (Pearcy et al. 1994). The retention of these characteristics would seem to indicate that it should still do well in high light environments, but though the plant responds positively to high light, ecologically it dominates in low light environments and is not normally found in full sun. Since light is a limiting factor for many species in forest understories, increased sunlight normally results in a higher density of vegetation (Daubenmire 1974) and a concomitant increase in competition for resources. Species adapted to full sun are able to outcompete shade-adapted species in high light environments (Grime 1994). So even though *M. vimineum* has some full sun adaptations allowing it to utilize high levels of sunlight, it still may not be able to compete in high light environments with plants specifically adapted to full sun.

Responses to Density and Intraspecific Competition

The correlations showing density decreasing with sunlight and plant biomass increasing with sunlight indicate that intraspecific competition may be fairly intense in this grass. A direct correlation between mean plant biomass and density cannot be made since values for mean plant biomass were derived mathematically from density values. However, in reviews of classic studies on density effects in agricultural crops and weeds, Harper (1977) showed that density stress is often absorbed by reduction in, or abortion of, plant parts. In particular, density stress in these crops caused a reduction in the number of culms, number of leaves, and leaf length. Since the bulk of the seeds for the species studied were produced on terminal infloresences, a reduction in culms results in a reduction in seed number. At higher densities there appears to be a compensatory effect such that the loss in culms is offset in part by the excess of individuals. So a wide range in plant density rarely results in as large a range of flower or seed production.

In *M. vimineum*, number of culms, main culm length, and length of the 4th leaf from the top all decreased to some degree with increasing stand density. It may be that the reductions in these characters simply result from the reduced overall plant size in the high density sites. But reductions in these factors result in a reduced potential for seed production in individual plants, particularly fewer culms, since most seeds are produced on terminal inflorescences. Since the high density stands usually produced fewer seeds per unit area, this would support the idea that *M. vimineum* stands suffer from density stress. Loss of leaves is a common response in density stressed plants since there is a net

carbon loss when a plant has too many shaded leaves (Harper 1977). This net carbon loss results from a high ratio of respiration to carbon assimilation (Boardman 1977). However, Horton (1996) showed that the light level at which carbon loss from respiration was compensated for by carbon gain from photosynthesis in *M. vimineum* was very low. This low light compensation point would enable leaves to retain some value to the plant in terms of carbon assimilation even when hidden not only beneath the forest canopy, but also beneath a thick herbaceous layer. So for *M. vimineum*, plants in dense stands may retain heavily shaded leaves without detrimental effects to growth.

Greenhouse Experiment

Higher biomass in the full sun treatment over the shade treatment clearly indicates that *M. vimineum* is capable of utilizing high levels of sunlight. But several complications with the experiment prevented use of the soil moisture data. First, plants were allowed to grow very large before the treatments began, and since the experiment only ran for 36 days, most of the biomass is a reflection of growth before treatments were initiated. The delayed initiation of the experiment is compounded by the fact that the soil in the upper resource states took time to dry, reducing the real duration of treatments. Second, the value for biomass is dried plant material and cannot account for the difference between healthy and unhealthy vegetation. Plants in the upper resource states appeared to be drying out and were probably not accruing new biomass by the termination of the experiment. Conversely, biomass accumulation in plants in the lower

resource states might not have suffered from the effects of flooding immediately. Compounding these problems, no absolute measurements were made of the soil moisture values, so there are no data for the actual soil moisture levels making comparisons to field data impossible.

It is odd that the plants died after harvesting since management records state that mowing does not kill it (Barden 1991). The plants were clipped 12.7 cm above soil level, which is considerably higher than mowing height and sufficient to leave nodes for new growth to sprout. Heavy mortality occurred in all soil resource states and in both light treatments, though the full sun treatment appeared to lose a greater volume of mass. This suggests that clipping should be further investigated to determine its effects on the species.

Flowering Strategy

Flowering strategy has important implications for population structure, including genetic variation in offspring, pollination success and probability of seed dispersal (Lord 1981, Cheplick 1998). Few or no CH flowers formed in the six main study sites, indicating that inbreeding and limited dispersal is common for *M. vimineum*. Among weedy or colonizing plants, selfing is considerably more common than outcrossing since selfing generally results in higher fecundity (Price and Jain 1981). In grasses, selfing through CL flowers is associated with ruderals and is thought to have evolved from CH flowers as a means of maximizing seed production (Campbell et al. 1983).

Flowering strategy appears to be plastic in *M. vimineum*, as evinced by the correlation of CH flowers and plant biomass. For many species the proportion of CH flowers increases under environmental conditions that enhance plant growth (Le Corff 1993, Wilken 1982, Waller 1980, Clay 1982, Bell and Quinn 1987). By producing CH flowers only in large plants which will produce many seeds, individuals reduce the risk of lower pollination success of CH flowers. However, the proportion of flowers in *M. vimineum* did not change in favorable light and soil moisture environments. Plant biomass and proportion of CH did increase in disturbed habitats. A possible explanation for this is that disturbance eliminates some individuals and reduces competition for resources. With less competition, plants may grow large even under low light and soil moisture.

A major advantage to producing CH flowers is increased potential for seed dispersal (Cheplick 1998). No obvious dispersal mechanisms exist for seeds of *M. vimineum*, but the seeds are small enough that they may cling by hydrostatic tension to wet surfaces. Seeds have been observed clinging to the seams of wet pants and boots (pers. obs.). These seeds could only have come from CH flowers or from CL flowers that had been damaged so that the seeds fell out of the sheath. This exposure might enable them to disperse a great distance from the parent if they are picked up by an animal or be transported by runoff or wind. For large plants which produce many seeds, the advantage in producing terminal CH flowers would be lessened sibling competition while still producing many seeds that will probably stay in the maternal environment (Cheplick

1993). In disturbed habitats, producing CH flowers potentially enables plants to colonize recently opened space by dispersing seeds into the new habitat.

Seed Production

Since *M. vimineum* is an annual, it is completely dependent on its seedbank for regeneration from year to year. *M. vimineum* produced very small seeds in profuse numbers and seed production increased linearly with increasing biomass of individuals. Large individuals produced hundreds of seeds, while extremely small plants produced only a few. The only plants that did not produce seeds were those that had been physically damaged subsequent to flowering. The close correlations between number of leaves per plant and sum culm lengths are also indicative of the importance of plant size to seed production. Since flowers in the stands were nearly all CL, high seed production creates not only intraspecific competition, but intense competition between siblings (Cheplick 1993).

Seed Germination and Viability

Two separate studies concluded that *M. vimineum* creates a seedbank that lasts 3-5 years or more (Barden 1987, Woods 1989). These conclusions were based on field observations in which seeds were left in a natural environment. However, in the laboratory germination experiments intended to determine what percentage of seeds germinated the first year, all of the viable seeds germinated, indicating that dormancy is

not innate. Dark-induced dormancy commonly occurs in seeds of many species buried in the soil (Wesson and Wareing 1969), but *M. vimineum* seeds germinated as readily in the dark as in fluorescent light. Dormancy in grasses may be induced or enforced by other environmental conditions including drought, high CO_2, low O_2, or extreme temperatures (see Simpson 1990). It is also possible that the method of collecting, stratifying, or storing the seeds may have scarified them and interrupted the dormancy mechanism. Regardless, the field and laboratory results are in direct conflict. Further study is needed to determine the mechanism of dormancy in *M. vimineum*, and if it indeed does form true seedbanks.

Lack of embryo development and reduced viability in RMF and MBC may have been caused by the late summer drought that occurred as the plants were producing seed. The plants in both RMF and MBC visually appeared to be suffering drought stress in September and October as the seeds were developing. In fact, by the end of the season, the plants in both these two sites were beginning to turn brown and wither. Lack of water may have caused mortality in the plants before the seeds set, or may have physiologically prevented the plants from utilizing internal resources to develop viable seeds. RMF suffered more from the drought than the other sites because it was in direct sunlight and consequently it had the lowest embryo development and seed viability percentages. Reduced seed output may be a factor contributing to absence of *M. vimineum* in full sunlight as late summer drought is common in the region and heat stress from sunlight exacerbates drought effects.

Conclusion

M. vimineum is a shade-tolerant grass that responds positively to sunlight, but is excluded from sunny habitats by a combination of sensitivity to lack of soil moisture and by an inability to compete with plants adapted to high light environments. It produces many seeds, most of which are produced on CL flowers and are not dispersed great distances. Individuals co-exist in strong competition, and some stands are so dense as to prevent growth of other plants. It can change flowering strategy to adapt to local conditions and this ability perpetuates the stands and enables it to spread to new habitats when disturbances give it the chance to gain a foothold.

Although it is not a strong competitor in full sun, its fecundity and growth form give it the potential to be a strong competitor in shady habitats. Its ability to grow tall and fall over, rooting at the nodes, could enable it to grow over other vegetation. Barden (1987) found that *M. vimineum* was not able to invade an existing stand of Japanese honeysuckle, another exotic that forms very dense stands in shady habitats. Nevertheless, *M. vimineum* can easily invade disturbed or otherwise unoccupied habitats and it seems likely that *M. vimineum* could also invade shady areas where the herbaceous layer is not dense enough to prevent it from becoming established. It is in these situations where *M. vimineum* could pose the greatest threat to native plant populations since once it becomes established, it appears not to relinquish space for other species.

Since *M. vimineum* invades most often after a disturbance eliminates other vegetation, it is difficult to determine which plant species *M. vimineum* is threatening, if

any. It reduces habitat available to native plants, but there are no records of it directly eliminating other plants from any area. It does form very dense stands, and within these stands biomass of other species is reduced with increasing densities of *M. vimineum*. Dyer and Rice (1997) showed that the native needlerush *Nassella pulchra* was eliminated when invading grasses reached high densities. In lower light sites in GSMNP, biomass of species other than *M. vimineum* was usually zero or extremely low. In forest canopies in the southern Appalachians, much of the herbaceous layer is fairly sparsely vegetated whether *M. vimineum* is present or not. It may be that *M. vimineum* has found an open niche and exploited it, or it may be that *M. vimineum* is displacing native plants. Documentation of *M. vimineum* depressing a native plant would require having vegetation records for an area before a disturbance enables *M. vimineum* to invade.

It seems that *M. vimineum* must require disturbance for a foothold in any new environment. It is most often found in disturbed habitats, and can be seen creeping along roads and trails that are mowed or trampled. All of the study sites had been disturbed at some point in the past. The forested stands were probably pasture or cropland before the inception of GSMNP, and were returned to forest 60 years ago when the land was made public property. *M. vimineum* probably became established as the cleared land turned to forest, before other herbaceous plants recolonized. With *M. vimineum* established, it is unlikely that other plants will have the opportunity to return. Even the high light sites, where *M. vimineum* was growing in competition with many other plants, were disturbed, enabling *M. vimineum* to become established. There are no adequate records of these

sites from which to conceptualize stand history, so there is no way of knowing whether *M. vimineum* is increasing or decreasing in these sites. Long term studies on stands would need to be conducted to quantify the damage done to native species and to determine if *M. vimineum* will persist in the habitats it has invaded.

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