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TRADING RESISTANCE FOR VIGOR:

A POTENTIAL MECHANISM FOR INVASION BY THE ASIAN GRASS *MICROSTEGIUM VIMINEUM*

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

By

MATTHEW ROBERT DICKINSON

B.S., University of Illinois at Chicago, 2008

2012
Wright State University

WRIGHT STATE UNIVERSITY
SCHOOL OF GRADUATE STUDIES

April 17, 2012

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Matthew Robert Dickinson ENTITLED Trading resistance for vigor: a potential mechanism for invasion by the Asian grass *Microstegium vimineum* BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Dickinson, Matthew Robert. M.S., Department of Biological Sciences, Wright State University, 2012.
Trading resistance for vigor: a potential mechanism for invasion by the Asian grass *Microstegium vimineum*.

The Evolution of Increased Competitive Ability (EICA) hypothesis predicts that subsequent to introduction, non-native plants escape enemies and selection favors genotypes that invest more in growth and reproduction and less in resistance. Here, I evaluated if the invasive Asian grass *Microstegium vimineum* has developed decreased resistance in its introduced range of the eastern US, as predicted by the EICA hypothesis. Asian and US genotypes were evaluated for differences in enemy damage, leaf toughness, specific leaf area (SLA), and flowering in a common garden experiment. Leaf damage, SLA, and flower production were greater and leaf toughness lower in US plants. These results, along with the previously reported faster growth of US populations, appear to support the EICA hypothesis. However, a common garden study should be conducted in the native range to evaluate if differences between US and Asian genotypes were influenced by environmental conditions of the introduced range.

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Acknowledgements-

I owe thanks to a number of people for their contributions to my Master’s thesis. I would like to briefly state the contributions of these individuals. My advisor, Volker Bahn, supported and guided me throughout my time as a Master’s student. Robert Warren familiarized with me the study area and helped me choose field sites. Luke Flory obtained and shared *Microstegium vimineum* seeds, which were essential to this project. Mark Bradford provided me with the opportunity to use the facilities and resources at Coweeta Hydrologic Laboratory. My thesis committee, John Stireman and Don Cipollini, supported and advised me throughout my Master’s program. All of these aforementioned people contributed to the design of my thesis project. Chelcy Ford and Joe Davis took care of my plants in the Coweeta greenhouse while I was not there to do so. Jeremy Heath assisted me in designing the leaf toughness test. DJ Shontz and Evangeline Shank weighed plant samples at Wright State University. Shishir Adhikari maintained plants in the Wright State University greenhouse while I was away doing field work. I greatly appreciate the help all of these people provided.

INTRODUCTION

Invasive plant species, non-natives that are highly successful in their introduced environment, are a large threat to the biodiversity of native communities because of their ability to modify ecosystems and out-compete native plant populations (Vitousek 1990, Wilcove et al. 1998). Understanding how invasive plant species spread and persist is essential for their prevention and control (Keane and Crawley 2002). Having knowledge of the processes by which non-native plants invade is necessary for identifying which exotics have potential to invade (Hierro and Callaway 2003), identifying areas susceptible to invasion (Lonsdale 1999), and predicting invasive species' response to environmental change (e.g. climate change and disturbance) (Rahel and Olden 2008). Other benefits include the ability to inform land use decisions and determine effective eradication methods.

In their introduced environment, exotic plants often encounter novel abiotic and biotic interactions. Biotic interactions include interspecific competition and attack by enemies (i.e. pathogens and herbivores). Selection pressure on an exotic species shifts due to these novel interactions (Lee 2002). Such shifts may accordingly alter a plant’s allocation of resources, an example of which is allocation away from traits that deter enemies and toward growth and reproduction in the event of a reduction in enemy atttack (Blossey and Nötzold 1995).

Enemies and exotic plant invasions

Enemies can play an important role in exotic plant invasions. A lack of herbivores and pathogens in the introduced range may provide a non-native with a competitive advantage over native species, as stated by the Enemy Release Hypothesis (Darwin 1859, Williams 1954, Elton 1958, Keane and Crawley 2002). On the other hand, enemies may prevent invasion by attacking the introduced species equally or even preferentially (Elton 1958). According to the Enemy Release Hypothesis, exotic plants escape specialist enemies but are not necessarily released from generalists in the introduced range (Keane and Crawley 2002).

Little or no enemy attack on an exotic plant subsequent to introduction may result in improved performance via rapid adaptive evolution (Blossey and Nötzold 1995, Maron et al. 2004). The Evolution of Increased Competitive Ability (EICA) hypothesis postulates that, subsequent to enemy release, selection pressure favors genotypes of exotic plants that allocate resources away from costly resistance traits (i.e. defenses that deter specialist enemies) and toward fitness-related traits, such as growth and reproduction (Blossey and Nötzold 1995). The EICA hypothesis can be tested by comparing progeny of native and introduced conspecifics in common environments and evaluating differences in vigor and defense (Bossdorf et al. 2005).

In tests of the EICA hypothesis, native and introduced genotypes should be compared in multiple common gardens across environmental gradients to evaluate if genotype by environment interactions contribute to performance differences (Flory et al. 2011b). For example, if introduced genotypes have lower resistance than native genotypes in a single common garden, it is impossible to determine if introduced genotypes have diminished defense regardless of the habitat or if introduced genotypes only have lower resistance than native genotypes under particular environmental conditions.

A number of common garden studies comparing defense and competitive ability between invasive and native genotypes have been performed in the introduced range

(Clement 1994; Blossey and Nötzold 1995; Willis et al. 1999; Buschmann et al. 2005; Joshi and Vrieling 2005; Statsny et al. 2005; Beaton et al. 2011). Some studies' findings were consistent with the EICA hypothesis' prediction of improved performance and reduced resistance (Blossey and Nötzold 1995, Joshi and Vrieling 2005, Beaton et al. 2011), while others were not (Clement 1994, Willis et al. 1999, Buschmann et al. 2005, Statsny et al. 2005). Of the studies that observed increased performance and reduced resistance, Joshi and Vrieling (2005) used 13 native and 16 introduced populations while others only included one or two populations from one or both origins (Blossey and Nötzold 1995, Beaton et al. 2011). Joshi and Vrieling (2005) included a sufficient number of populations for testing the EICA hypothesis, but only compared genotypes in a single common garden.

The EICA hypothesis and *Microstegium vimineum*

Here, the resistance of and enemy attack on the invasive Asian grass *Microstegium vimineum* (Trinius) A. Camus was studied in its introduced environment to evaluate EICA as an explanation for the plant's invasiveness. Among the negative effects *M. vimineum* has on its introduced habitat are a reduction in herbaceous plant biomass and diversity (Flory and Clay 2010a), hindrance of forest succession (Flory and Clay 2010b), and alteration of soil properties and nutrient cycling (reviewed by Warren et al. 2010).

The opportunity for a direct comparison of invasive and native *M. vimineum* for genetic differences was afforded by colleagues' collection of seeds from populations spanning both its introduced range in the eastern US and its native Asian range. As a full test of the EICA hypothesis requires comparison of native and introduced genotypes in both ranges (Hierro et al. 2005), and a native range study has yet to be conducted, this study, in conjunction with work by Flory et al. (2011a, b), is a first step towards testing the EICA hypothesis on *M. vimineum*. While *M. vimineum* appears to be common in its native range, it is rarely locally abundant (SL Flory pers. comm.), suggesting improved success in the introduced range.

Previous studies indicated genetic differentiation of *M. vimineum* between its native and introduced ranges (Flory et al. 2011a, b). Greater biomass was found in introduced *M. vimineum* in greenhouse and common garden experiments in which progeny of introduced and native populations were compared. As an annual plant, *M. vimineum*'s success depends on reproductive output; however, Cheplick (2008) and Warren et al. (2011b) reported a strong positive correlation between seed production and growth in *M. vimineum*, indicating that biomass is a good proxy for fitness in *M. vimineum*.

Enemy attack on *M. vimineum* was not reported until recently (Bradford et al. 2009; Kleczewski and Flory 2010; (Y Tang, RJ Warren, TD Kramer, and MA Bradford unpublished data). Kleczewski and Flory (2010) found that a fungus of the genus *Bipolaris* caused leaf blight disease in *M. vimineum* near Arnoldsburg, WV. In Athens, GA, Bradford et al. (2009) observed that insects, including orthopterans (grasshoppers, katydids, and crickets) and hemipterans (stink bugs and bordered plant bugs), fed on *M. vimineum*.

The herbivores and pathogens that attack *M. vimineum* in the introduced range are likely generalists and not specialists. Specialist enemies are those that coevolved with the host plant in their native habitat (Keane and Crawley 2002). However, specialist enemies may be present in the invaded environment if they were introduced as well. Specialist enemies in the introduced range could also occur through host-switching, in which a specialist of a closely related species in the introduced habitat adopts the invasive plant as a host (Keane and Crawley 2002). Host-switching is unlikely in the case of *M. vimineum* because no other species of the genus *Microstegium* are present in the US (Flory et al. 2011b).

The relatively long timeframe between *M. vimineum*'s first US detection in 1919 (Fairbrothers and Gray 1972) and its identification as an invader in the 1980s (Barden 1987) is consistent with the theory of EICA (Flory et al. 2011b). The apparent lag between introduction and spread as an invader may have resulted from a period of adaptation to its novel environment, free of specialist enemies, in which *M. vimineum* evolved to reduce its investment in resistance while increasing its investment in competitive ability.

Study Goals

The goal of this study was to evaluate if the EICA hypothesis is applicable to *M. vimineum.* I determined if *M. vimineum*'s greater growth resulted from a reduced investment in defenses as a trade off, and if this trade off corresponded to increased enemy susceptibility, as predicted by the EICA hypothesis.

This study goal was accomplished by comparing resistance and enemy damage in the progeny of *M. vimineum* populations from its native and introduced ranges. Resistance was quantified with measures of leaf toughness and specific leaf area, which are inversely related traits (Witkowski and Lamont 1991, Choong et al. 1992) that are associated with defense against both specialist and generalist herbivores (Jordano and Gomariz 1994, Coley et al. 2006). A difference in the resistance-related traits between native and introduced *M. vimineum* genotypes would indicate genetic differentiation, which is a prerequisite for EICA. Genetic differentiation was further examined by evaluating introduced and native genotypes for variation in inflorescence phenology. From here forward progeny of native and introduced populations of *M. vimineum* will be referred to by seed origin (Asia and US, respectively).

If EICA did contribute to invasion, *M. vimineum* must have (1) experienced enemy release upon introduction to the US and (2) evolved to allocate resources away from resistance and towards growth and reproduction. I contributed to evaluating the EICA hypothesis on *M.* vimineum by addressing one concrete question, along with four associated hypotheses.

Is there a difference in enemy damage and leaf toughness between Asian and US *M. vimineum*? Given the knowledge that US plants grow faster than Asian plants (Flory et al. 2011a, b) and that this increase in vigor may have come at the cost of less energy available for overall defenses, I can deduce four alternative hypotheses regarding investment in defense: H1) US *M. vimineum* has evolved a reduced investment in defenses against specialists but has maintained leaf toughness as a defense against generalists. Consequently, generalist damage and leaf toughness will be similar among US and Asian plants. H2) US *M. vimineum* evolved additional leaf toughness to deter generalists but was still able to obtain higher vigor by reducing other costly defenses against specialists. As a result, Asian plants must have lower leaf toughness and greater damage inflicted by generalists than US plants. H3) US plants evolved reduced defenses against specialists and reduced leaf toughness as resistance against generalists. Consequently, damage would have to be lower and leaf toughness higher in Asian plants than in US plants. In this scenario, leaf toughness may act as a defense against specialists in addition to generalists. H4) US plants have decreased their investment in leaf toughness while increasing their investment in other, here unmeasured, inexpensive defenses against generalists. In this case, damage and leaf toughness would be greater in Asian plants and leaf toughness may be a resistance trait effective against both specialists and generalists.

METHODS

The study aim of determining if invasive *M. vimineum* has developed a reduced investment in resistance and an increased susceptibility to enemies was achieved by assessing US and Asian *M. vimineum* for differences in leaf damage, leaf toughness, and specific leaf area (SLA). Phenological differentiation was evaluated by examining US and Asian plants for variation in inflorescence production. The progeny of multiple populations from the US and Asia were compared in a common garden experiment in southwestern North Carolina, where *M. vimineum* is invasive and has been observed to experience damage by herbivores and disease (Y Tang, RJ Warren, TD Kramer, and MA Bradford unpublished data).

Study species

Microstegium vimineum (common names include Japanese stiltgrass and Nepalese browntop) is an annual C_4 grass native to southeastern Asia that has invaded the eastern US (Warren et al. 2010). Since appearing in Knoxville, TN in 1919 (Fairbrothers and Gray 1972), the grass has spread to 25 states (USDA 2010). Traits of *M. vimineum* which are characteristic of invasive plants include a high seed output (100-1000 per plant), a persistent seed bank (up to three years), a high level of phenotypic plasticity, self-fertilization, and an annual life history (reviewed by Warren et al. 2010). *M. vimineum* grows and reproduces best with high light availability, high soil moisture, and sparse leaf litter and is usually found along waterways, roads and in disturbed areas (Warren et al. 2011a). Moreover, this invasive grass is shade tolerant and can persist in forest understories (Horton and Neufeld 1998). *M. vimineum* is not wind-dispersed but may be dispersed by animals (Flory et al. 2011a); in addition, stormwater run-off can disperse seeds up to 15 m (Warren et al. 2011a).

Seed collection and study sites

M. vimineum seeds were collected from 2008 to 2011. US seeds were collected from ten populations across nine states in the eastern US (Table 1, Figure 1). Asian seeds were collected from nine populations in three provinces of China and one population in Japan (Table 1, Figure 2).

The common garden experiment was conducted in Macon County, NC. Five common garden plots were constructed at Coweeta Hydrologic Laboratory (CHL) (35°03' N; 83°25' W) and three at Tessentee Bottomland Preserve (TBP) (35°04'03.57" N; 83°23'00.53" W). The common gardens were not deliberately placed in a specific selection of environments, but the placement of common gardens in different locations at an array of elevations allowed for evaluating if results depended on specific environments or held true across a range of conditions (Table 2, Figure 3). Plots were installed within areas invaded by *M. vimineum* to increase the likelihood that enemy attack on study plants reflected damage inflicted on local *M. vimineum* populations.

Experimental design

On April 15, 2011, *M. vimineum* seeds were sown in Metro Mix 360 (Sun Gro Horticulture, Ltd., Bellevue, WA) in flats partitioned by 200 mL inserts in a greenhouse at CHL. Three seeds from the same population were sown in each insert. Labels noting the source population of the seeds

Table 1. Locations of seed source populations

Continent	#	Country	Province/State/ Prefecture	Nearest Town/County	Latitude	Longitude
Asia	1	China	Yunnan	Yaojie	23°55'48.00"N	101°39'24.00"E
Asia	2	China	Yunnan	Lijiang	24°03'29.00"N	101°57'54.00"E
Asia	3	China	Yunnan	Zhelong	24°18'10.00"N	101°21'50.00"E
Asia	4	China	Yunnan	Pindiang	24°03'32.00"N	101°57'53.00"E
Asia	5	China	Zheijiang	Changhua	30°10'29.35"N	119°11'56.47"E
Asia	6	China	Shanghai	Shanghai	31°05'38.76"N	121°11'51.36"E
Asia	7	China	Shanghai	Shanghai	31°11'32.03"N	121°21'33.59"E
Asia	8	China	Zheijiang	Lin'an	30°15'24.26"N	119°43'22.26"E
Asia	9	China	Shanghai	Chongming Island	31°31'52.50"N	121°51'52.38"E
Asia	10	Japan	Nara	*Unknown*	34°30'50.69"N	136°00'37.48"E
North America	1	US	North Carolina	Chapel Hill	35°53'24.24"N	79°00'55.65"W
North America	2	US	Maryland	Queenstown	38°55'21.60"N	76°09'07.38"W
North America	3	US	Pennsylvania	Bushkill	41°05'45.83"N	75°00'10.14"W
North America	4	US	South Carolina	Hopkins	33°48'27.70"N	80°51'55.40"W
North America	5	US	New Jersey	Oceanville	39°29'25.90"N	74°25'39.10"W
North America	6	US	West Virginia	Morgantown	39°39'45.00"N	79°58'60.00"W
North America	7	US	Indiana	Madison	38°59'14.00"N	85°22'46.00"W
North America	8	US	North Carolina	Madison Co.	35°44'44.63"N	82°40'26.04"W
North America	9	US	Ohio	Athens	39°19'46.31"N	82°06'04.37"W
North America	10	US	Connecticut	North Branford	41°22'29.00"N	72°45'32.00"W

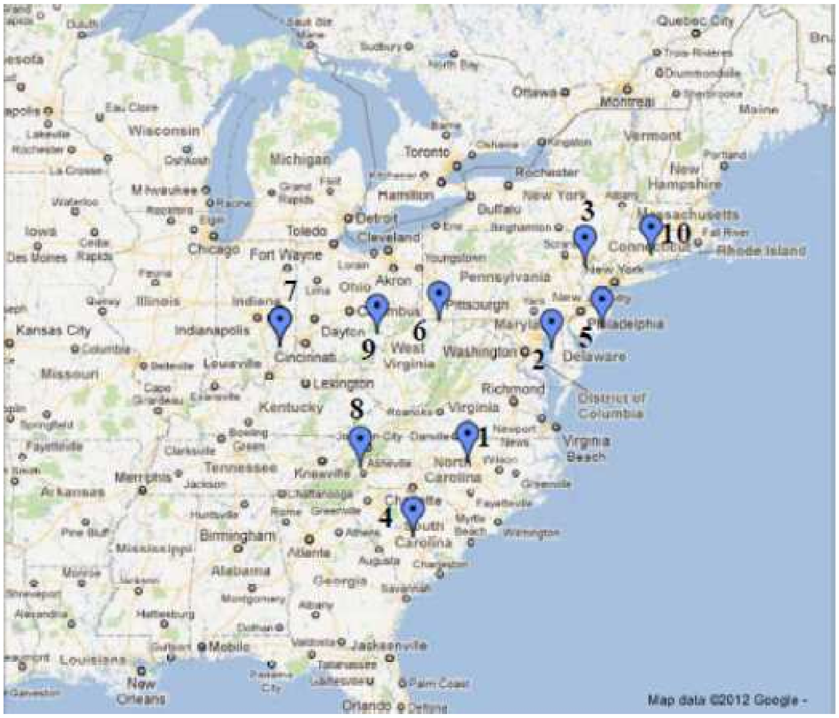


Figure 1. Locations of US seed source populations

Figure 2. Locations of Asian seed source populations

Table 2. Locations of study sites

Site	**Latitude**	**Longitude**	**Elevation**
1	35°04'11.66" N	83°23'02.27" W	634 m
2	35°04'07.64" N	83°23'04.96" W	645 m
3	35°04'02.61" N	83°22'48.20" W	647 m
4	35°04'05.34" N	83°26'30.98" W	853 m
5	35°04'08.40" N	83°26'31.04" W	721 m
6	35°03'49.75" N	83°26'24.14" W	718 m
7	35°03'48.99" N	83°26'23.81" W	690 m
8	35°03'39.23" N	83°25'51.44" W	689 m

Figure 3. Locations of study sites

were placed in each insert. Seeds were watered lightly for one minute intervals every 15 minutes by an automated sprinkler system. In the first week of May 2011, seedlings from each population were transplanted to field plots. At each of eight sites, four individuals from each of the 20 populations were randomly placed in a 1 m x 0.8 m grid with one plant per 0.1 m x 0.1 m cell for a total of 640 individuals. Labeled flags were placed adjacent to individual plants. After three weeks, seedling mortalities (US = 42/320, Asia = 41/320) were replaced with individuals from corresponding source populations that had been maintained in the greenhouse since the original planting. Unfortunately, the number of remaining greenhouse seedlings was not sufficient to replace all mortalities, reducing the sample size from 640 to 629.

Plant measurements

Leaf toughness offers resistance against herbivores (Jing and Coley 1990, Krischik and Denno 1990, Bergvinson et al. 1994) and is related to a variety of leaf characteristics, including cell to wall volume fraction, insoluble fiber content (i.e. cellulose, hemicellulose, and lignin), density, and specific leaf area (Choong et al. 1992, Choong 1996, Westbrook et al. 2011). In the fourth week of August 2011, the fourth leaf down from the top of a randomly selected tiller of each plant was sampled to measure leaf toughness. Leaves were placed in a cooler subsequent to sampling to minimize dehydration.

The leaf toughness test was performed using the penetrometer technique, which measures the weight required to puncture a leaf (Tanton 1962). Leaves were secured over a piece of corkboard with a 3 cm-diameter hole. The corkboard and leaf sample were placed on a balance. I used a micromanipulator to slowly lower a 1 mm-diameter cylindrical rod into an area of the leaf lying over the corkboard hole. The point on the leaf to be penetrated was approximately at the midpoint of the leaf’s length and halfway between the midrib and the leaf’s edge. The weight applied by the rod immediately prior to penetration of the leaf was recorded and converted to pressure using the equation $P = 9.807M/A$, where P is pressure (MPa), 9.807 m/s^2 is standard gravity, M is the mass (g) required to puncture the leaf, and A is the area (mm^2) of the rod's base (Gallardo and Merino 1993, Quinn et al. 2000).

Leaves were sampled for damage assessment as plants were harvested in the third week of September 2011. Preliminary surveys indicated that a sub-sample of 15 leaves per individual sufficiently represented damage sustained by the whole plant. Every other leaf was sampled from as many tillers as necessary to obtain 15 leaves. I chose tillers from different parts of a plant so that leaves sampled were representative of the entire plant. Leaves less than approximately 1.5 cm in length and/or containing brown coloration from nutrient stress, dehydration, or senescence were excluded because the damage assessment software would have classified the brown areas as enemy damage. If an individual had fewer than 15 leaves, all leaves present were sampled. However, plants with 5 or fewer leaves were not included in the damage assessment. Subsequent to sampling, leaves were stored in a cooler to preserve freshness. Leaves were scanned with a Microtek ScanMaker 4900. All leaves sampled from an individual were included in a single digital image. The percent leaf damage per plant was determined using Assess 2.0 Image Analysis Software for Plant Disease Quantification (Lakhdar Lamari, Saint Paul, MN). Leaf damage was classified as interior chewing, edge chewing, leaf mining, or leaf blight disease. I noted the presence or absence of damage types for each plant. Percent damage per leaf was calculated by dividing percent leaf damage per plant by the number of leaves sampled.

Leaves sampled for damage assessment were also used to calculate canopy specific leaf area (SLA) by dividing average leaf area per plant (as determined by Assess 2.0) by average leaf mass per plant. Low SLA values are associated with slower growing plants (Westoby 1998) that are better defended (Wright and Cannon 2001) and have longer lived leaves (Westoby 1998, Wright and Westoby 2002, Wright et al. 2004).

All aboveground plant material was harvested and dried to constant mass. However, flowering began earlier than expected and many plants lost biomass through dropped seeds and leaf senescence. Thus, biomass measurements were not included in the data analysis. Plant phenology was quantified by noting whether or not individuals had produced flowers at harvest.

Abiotic measurements

Soil moisture was measured on July 11 and August 10, 2011, while diffuse light was only measured on July 11 because the canopy cover, and therefore the amount of light reaching the plots, was not expected to change over the course of the growing season. Volumetric soil moisture was measured with a Hydrosense Soil Water Content Measurement system. Diffuse light (percent photosynthetically active radiation) was found by calculating the difference between understory measurements of photosynthetically active radiation (PAR) (using a LI-200 line quantum sensor) and fully exposed PAR readings (using a LI-200 spherical PAR sensor) from a reference site.

Statistical analysis

Mixed models were used to analyze percent leaf damage, leaf toughness, SLA, and flowering data because mixed models incorporate random effects. Random effects allow for interpretation of variables (e.g. seed source population) that are sampled from a larger population as a unified group that is representative of the variation within the larger population (Bolker et al. 2009). Leaf toughness data were normally distributed and leaf damage and SLA data were normalized via log transformation allowing for analysis of the three variables with linear mixed effects (LME) models. A generalized linear mixed model (GLMM) of the binomial family with a logit link was used to analyze the binary variable of flower production. To assess which configuration of independent variables (i.e. seed origin, seed source population, study site, soil moisture, and diffuse light) best explained the variation in the dependent variables of leaf damage, leaf toughness, SLA, and flower production, five series of models (Table 3) were evaluated. To confirm the importance of seed origin, top models of each dependent variable were evaluated without the fixed effect of origin. To determine if genotype by environment interactions were important, top models of each dependent variable were assessed with the inclusion of the random effect site by population interaction. Models were compared using Akaike information criterion (AIC) scores. LME models were fit using restricted maximum likelihood estimation and the GLMM models were fit with Laplace approximation. Differences in occurrence of damage types between US and Asian populations were assessed using a chi squared test.

If differentiation in the introduced range resulted from adaptive evolution, US populations would need to have had substantial genetic variance upon which selection could have acted (Lee 2002). Including populations from across the native range ensured that a variety of Asian genotypes were present in this study. If the variance among traits in US populations was similar to or larger than trait variance in Asian populations, I could assume that substantial genetic variance exists in the introduced range (Flory et al. 2011b). Lower variance in US populations' trait values would suggest that they experienced a genetic bottleneck or founder effect (Bossdorf et al. 2005). Barlett's test was performed to test for differences in variances in SLA, leaf toughness, and percent leaf damage between US and Asian genotypes.

If plants with lower SLA and higher leaf toughness have greater resistance, SLA and leaf toughness should be positively and negatively correlated, respectively, to percent leaf damage. Additionally, leaf toughness and SLA, which have been documented as associated leaf characteristics (Witkowski and Lamont 1991, Choong et al. 1992), are expected to be negatively correlated. To test for correlations, I evaluated leaf damage vs. leaf toughness, leaf damage vs. SLA, and SLA vs. leaf toughness with linear regression.

To determine if flowering time was dependent on the source populations' latitudes, I performed a regression of percent of individuals flowering per population against population latitude. Regressions using populations from both continents, as well as populations within each continent, were analyzed. Data was analyzed in the statistical programming environment R (R Development Core Team 2009).

Table 3. Model series (“x” indicates that the interactive relationship, in addition to the additive relationship, of two parameters were analyzed; a vertical line between two variables (e.g. origin|site) indicates that the random effect, which is to the right of the vertical line, interacts with a fixed effect, which is to the left of the vertical line).

Model Number	**Fixed Effect**	**Random Effect**
1A	Origin x Light x Moisture	Population
1B	Origin + Light x Moisture	Population
1C	Origin x Light + Moisture	Population
1D	Origin x Light x Moisture	Population
1E	Origin + Light + Moisture	Population
1F	Origin + Moisture	Population
1G	Origin + Light	Population
1H	Origin	Population
1I	Origin + Light + Moisture	N/a
1J	Origin + Light	N/a
1K	Origin + Moisture	N/a
1L	Origin	N/a
2A	Origin	(Origin|Site) + (Origin|Population)
2B	Origin	(Origin|Site) + Population
2C	Origin	Site + (Origin|Population)
2D	Origin	Site + Population
2E	Origin	Site
2F	Origin	Origin|Site
3A	Origin	((Light x Moisture)|Population)
3B	Origin	((Light + Moisture)|Population)
3C	Origin	(Light|Population) + (Moisture|Population)

4A	Origin + Light + Moisture	(Origin|Site) + Population
4B	Origin + Light + Moisture	Origin|Site
4C	Origin + Light + Moisture	Population
5A	Origin x Light x Moisture	(Origin|Site) + (Origin|Pop.)
5B	Origin x Light x Moisture	(Origin|Site) + Pop.
5C	Origin x Light x Moisture	Site + (Origin|Pop.)
5D	Origin x Light x Moisture	Site + Pop.
5E	Origin x Light x Moisture	Site
5F	Origin x Light x Moisture	Origin|Site

RESULTS

Percent leaf damage, specific leaf area, and flowering probability were greater in US plants and leaf toughness was higher in Asian plants (Figure 4). While SLA, leaf toughness, and percent leaf damage were similar between US and Asian plants at several study sites, Asian plants never had greater SLA, percent leaf damage, or flowering probability, or lower leaf toughness at a particular site (Figure 5). Models with a $\triangle AIC < 2$ ($\triangle AIC = AIC_x - AIC_{1,}$ where 1 refers to the model with the lowest AIC score and x is any given model) were considered strong competitors in explaining the variation in a particular dependent variable (Ripplinger and Sullivan 2008). Model results indicated that seed origin, seed source population, and study site were important factors in describing the variation in all dependent variables, and the interaction of site and population was important for specific leaf area (SLA), leaf toughness, and flower production (Table 4). The model of best fit for percent leaf damage showed that leaf damage varied among study sites and was higher on US than Asian plants (Table 4). The proportions of types of damage were independent of origin ($X^2_3 = 1.85$, $P = 0.6042$). The model of best fit for leaf toughness conveyed that leaf toughness varied by site and population, was greater in Asian plants, and decreased with diffuse light and soil moisture (Table 4). In addition to the individual influences of origin, light, and soil moisture on leaf toughness, the interactions between the three parameters were also important for describing leaf toughness variation meaning that the effect of origin was conditional on light and soil moisture. The top model for SLA showed that SLA was higher in US populations and varies between sites; study site also influenced the variation between seed origins in the SLA model of best fit (Table 4). The model of best fit for flower production showed that US plants produced more flowers and that flowering varied by site and population (Table 4). A significant correlation was found between percent of individuals flowering and latitude when all populations were included ($r^2 = 0.56$, $0.05 > P > 0.01$) but not when populations within continent of origin were analyzed (US: $r^2 = 0.38$, $P > 0.1$; Asia: $r^2 = 0.09$, $P > 0.1$). The regression of SLA against leaf toughness revealed a significant negative correlation ($r^2 = 0.06$, $P < 0.01$), while no relationships were found between either percent leaf damage and leaf toughness ($r^2 = 0.001$, $P > 0.1$) or percent leaf damage and SLA ($r^2 < 0.001$, $P > 0.1$). Percent leaf damage, and SLA variances were greater in US genotypes over Asian genotypes but leaf toughness variances did not differ (percent leaf damage: $K^2 = 4.27$, df = 1, $P = 0.04$; SLA: $K^2 = 9.21$, df = 1, $P = 0.002$; leaf toughness: $K^2 = 0.04$, df = 1, $P = 0.85$).

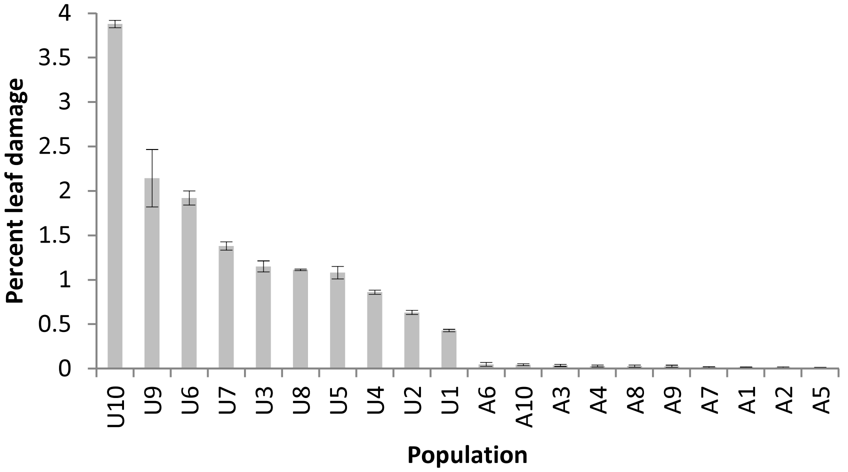
DISCUSSION

Understanding how non-native plant species invade their introduced habitat is necessary for determining appropriate management actions, such as preventing establishment and controlling the spread of invasive species. One explanation for exotic plant invasion is described by the Evolution of Increased Competitive Ability (EICA) hypothesis. This theory predicts that exotic species escape specialist enemies in their introduced habitat and, subsequently, selection favors genotypes that invest more in growth and reproduction and less in

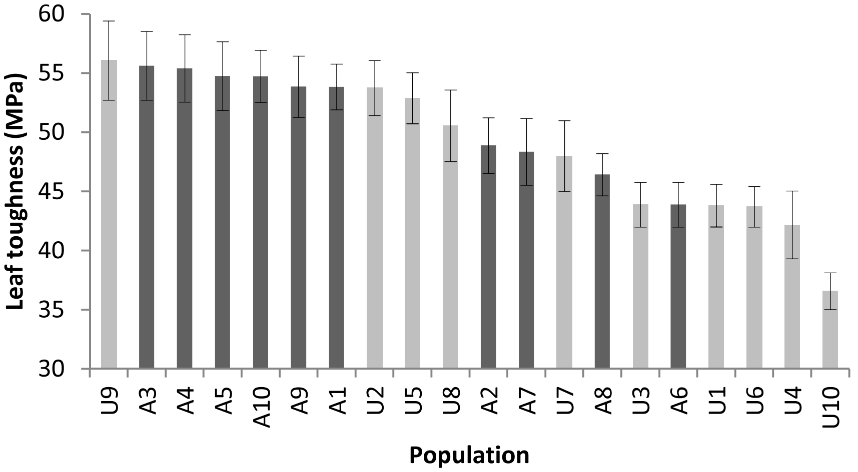
Table 4. Models of best fit. Shown are models with △AIC < 2 for each of the four dependent variables (LME = linear mixed effect, GLMM = generalized linear mixed model, pop. = population; “x” indicates that the interactive relationship, in addition to the additive relationship, of two parameters were analyzed; a vertical line between two variables indicates that the random effect, which is to the right of the vertical line, interacts with a fixed effect, which is to the left of the vertical line).

Dependent Variable	Model Type	Fixed Effect	Random Effect	△AIC
Specific Leaf Area	LME	Origin	Origin|Site	0.00
	LME	Origin	Pop. + (Origin|Site)	0.17
	LME	Origin	(Origin|Site) + (Site x Pop.)	0.37
	LME	Origin	(Origin|(Site x Pop.)) + Pop. + (Origin|Site)	1.62
Leaf Toughness	LME	Origin x Moisture x Light	Site + Pop.	0.00
	LME	Origin x Moisture x Light	Site + Pop. + (Site x Pop.)	0.12
Percent Leaf Damage	LME	Origin	Site	0.00
	LME	Origin	Site + Pop.	0.54
Flower Production	GLMM	Origin	Site + Pop.	0.00
	GLMM	Origin	Site + (Origin|Pop.)	0.68
	GLMM	Origin	Site + Pop. + (Site x Pop.)	1.53
	GLMM	Origin + Moisture	Site + Pop.	1.93
	GLMM	Origin + Light	Site + Pop.	1.96

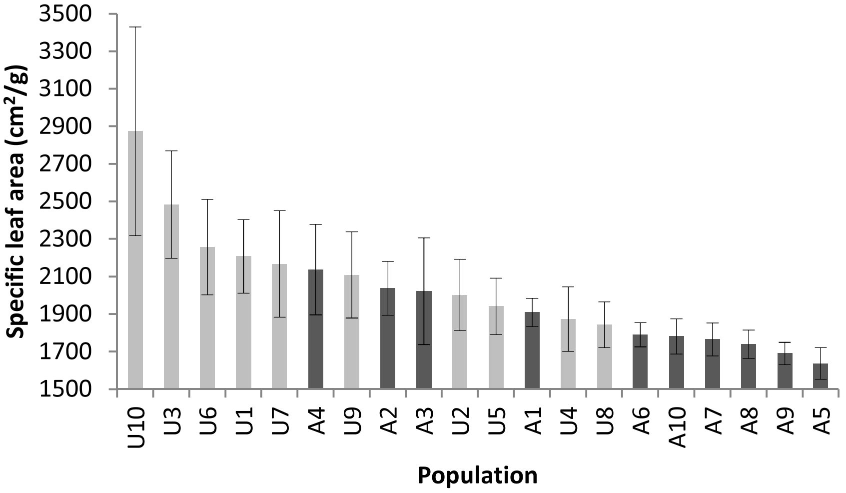
A)


Percent leaf damage
4
3.5
3
2.5
2
1.5
1
0.5
0
U10
U9
U6
U7
U3
U8
U5
U4
U2
U1
A6
A10
A3
A4
A8
A9
A7
A1
A2
A5
Population

B)


Leaf toughness (MPa)
60
55
50
45
40
35
30
U9
A3
A4
A5
A10
A9
A1
U2
U5
U8
A2
A7
U7
A8
U3
A6
U1
U6
U4
U10
Population

C)



D)

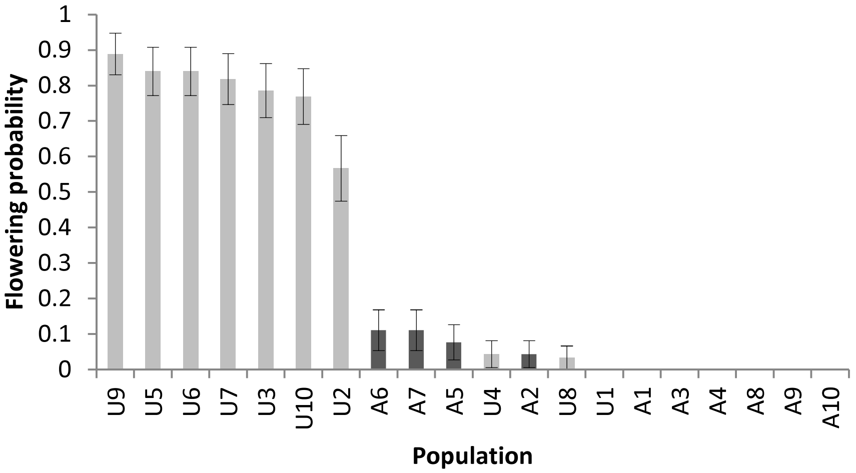
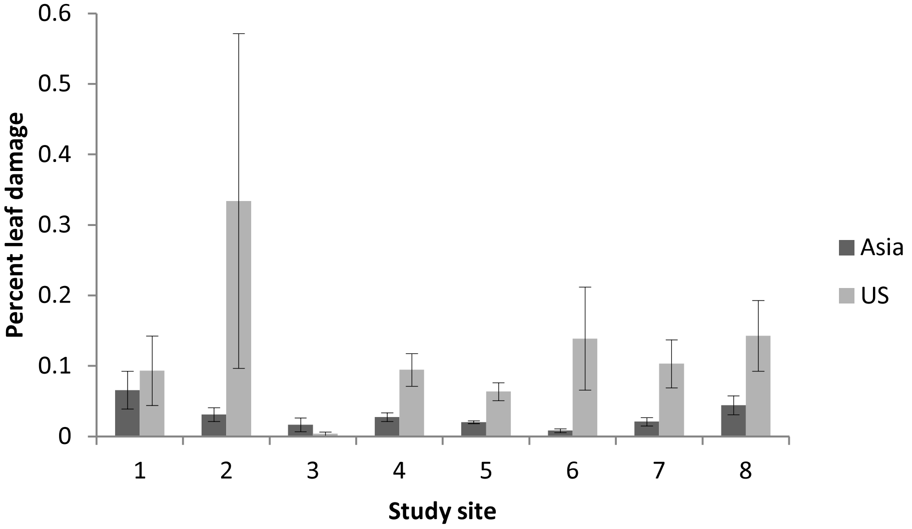
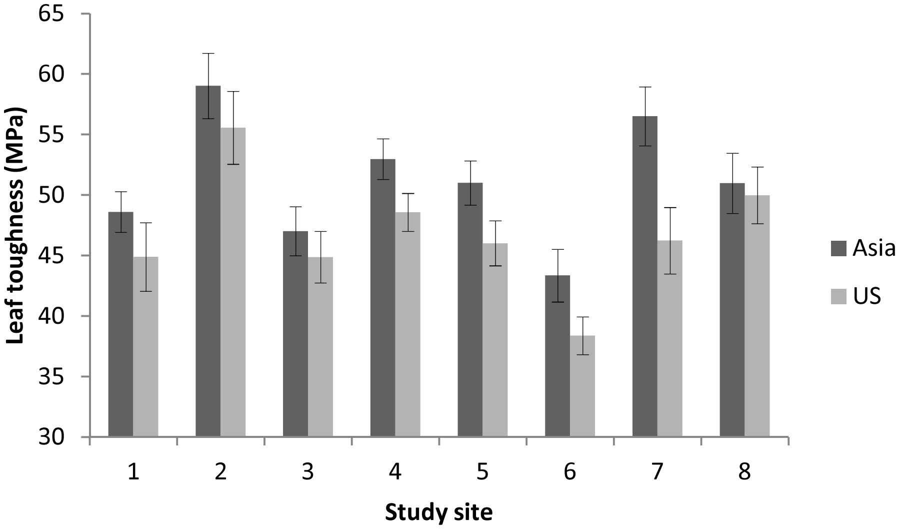


Figure 4. Percent leaf damage, leaf toughness, specific leaf area, and flowering probability by population. Values are population means with standard errors; populations are positioned along the x-axis in descending order by value from left to right (U = US and A = Asia).

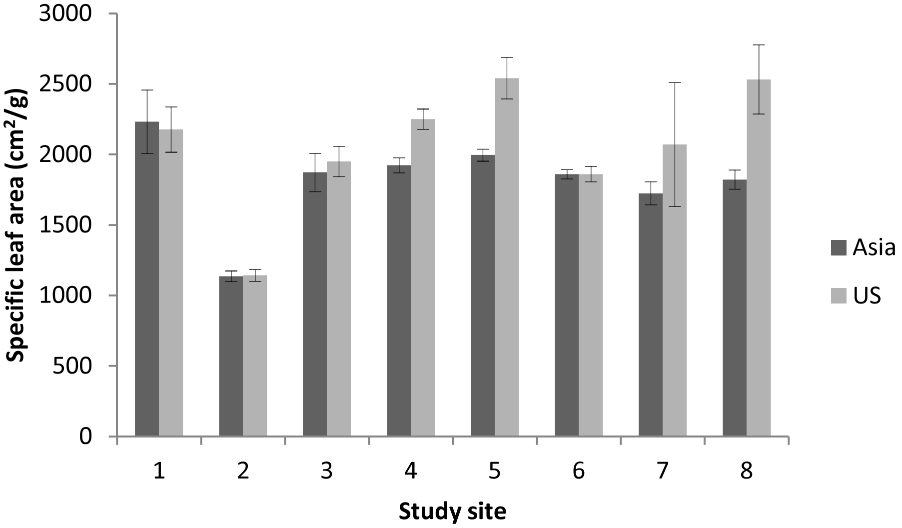
A)


0.6
0.5
0.4
0.3
0.2
0.1
0
Percent leaf damage
1
2
3
4
5
6
7
8
Study site
Asia
US

B)


65
60
55
50
45
40
35
30
Leaf toughness (MPa)
1
2
3
4
5
6
7
8
Study site
Asia
US

C)



D)

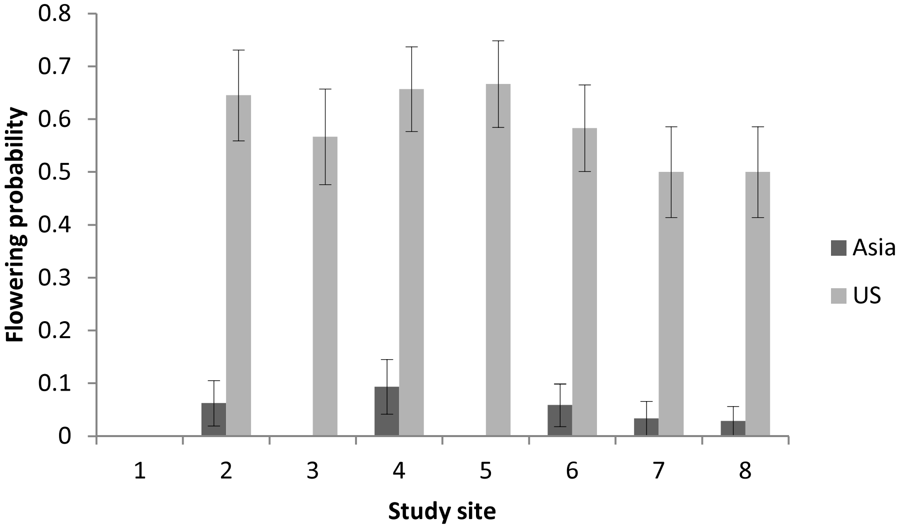


Figure 4. Percent leaf damage, leaf toughness, specific leaf area, and flower production by study site. Values are site means with standard errors.

resistance. Here, I evaluated if the increased growth of introduced *Microstegium vimineum* found by Flory et al. (2011a, b) resulted from a reduction in resistance. The lower leaf damage, greater leaf toughness, and lower specific leaf area (SLA) in native (Asian) vs. introduced (US) populations of *M. vimineum* support hypothesis H3: US *M. vimineum* evolved a reduced investment in defenses against specialist enemies as well as reduced leaf toughness as defense against generalist enemies. However, a lack of relationship in both leaf toughness and SLA to percent leaf damage suggests that a reduction in other resistance-related traits in addition to leaf toughness and SLA is responsible for the greater damage inflicted on US genotypes. Still, the most parsimonious explanation for higher leaf damage in US populations is a reduction in resistance. The earlier flowering of US *M. vimineum* provides further evidence of genetic differentiation, a necessary condition of the EICA hypothesis, and may be related to the faster growth of US populations' found by Flory et al. (2011a, b).

Enemy attack

According to the EICA hypothesis, invasive plants escape specialist enemies and evolve to allocate resources away from resistance and towards growth and reproduction (Blossey and Nötzold 1995). However, generalists may attack invasive species in the introduced range (Keane and Crawley 2002).

Two alternate theories that are not exclusive of the EICA hypothesis may assist in understanding the lower generalist attack rates on Asian *M. vimineum*: the Behavioral Constraint Hypothesis and the Novel Defense Hypothesis (Lankau et al. 2004). The Behavioral Constraint Hypothesis (BCH) predicts that a lag in herbivore attack occurs because adaptive evolution of feeding behavior must take place in order for herbivores to include an unfamiliar plant (in this case, native *M. vimineum*) in their diet. The Novel Defense Hypothesis (NDH) predicts reduced herbivore attack on a novel food source prior to generalists’ evolution to overcome resistance traits or the plants' evolution of reduced investment in resistance.

The NDH's prediction that herbivory increases subsequent to evolution of reduced resistance is the most parsimonious explanation for the greater feeding rates on US genotypes. Under the BCH, generalists' reduced attack on Asian *M. vimineum* resulted from a lack of herbivore adaptation. However, generalist feeding is by definition plastic (Bernays and Chapman 1994) and it is unlikely that generalist herbivores prefer US genotypes over Asian genotypes because of recognition of a difference between the two prior to consumption. The lower feeding on Asian plants is more likely a response to Asian genotypes' greater resistance and lower palatability. I found no difference in the proportions of different damage types between US and Asian plants, indicating that the difference in defense investment had similar effects across different types of enemies. While the relative contribution of each damage type to percent leaf damage was not quantified, greater disease on US *M. vimineum* could result from transmission of pathogens by herbivores (Kluth et al. 2002) and/or a reduced investment in disease resistance traits.

Resistance and leaf morphology

The lower leaf toughness and greater SLA in US populations offer evidence for a differentiation in leaf structure in the introduced range. The inverse relationship between SLA and leaf toughness observed here agrees with findings of previous studies (Witkowski and Lamont 1991, Choong et al. 1992).

Previous studies that used penetrometers to measure leaf toughness have reported a negative correlation between enemy attack rates and toughness (Jing and Coley 1990, Krischik and Denno 1990), including Bergvinson et al. (1994), who found that tougher leaves of the grass *Zea mays* were eaten less by the European corn borer. Choong and colleagues (1992, 1996) claimed that leaf toughness should be measured as the work, and not the weight or pressure, required to fracture a leaf. The primary argument against the penetrometer method is that thicker leaves increase toughness readings and that thicker leaves are not necessarily tougher (Choong et al. 1992). This issue may be resolved by correcting toughness measures against leaf thickness (i.e. dividing penetrometer toughness by leaf thickness) (Choong et al. 1992). However, thickness, as with toughness, should be measured on fresh leaf samples and the limited time in which leaves maintained freshness after being harvested prevented a measure of thickness subsequent to quantification of toughness.

The lack of a relationship between leaf damage and either leaf toughness or SLA suggests that the greater enemy attack on US populations resulted from a reduction in additional resistance-related characteristics, such as allelochemicals. Silica is an important compound in grasses that deters herbivores (Gurevitch et al. 2002, reviewed by Reynolds et al. 2009) and fungal pathogens (reviewed by Fauteux et al. 2005). Evaluating silica concentrations may be a worthwhile test for differences between *M. vimineum* populations in chemical defense.

Phenology and vigor

The earlier production of inflorescences by US plants may indicate greater fitness. A shorter lifespan in US plants, from earlier flowering and senescence, may be a strategy for dealing with the negative impact of an increased enemy load in response to decreased resistance (Minchella 1985, Hochberg et al. 1992). The inverse relationship between lifespan and growth (Garnier 1992, West et al. 1997, Marbà et al. 2007) suggests that US plants' earlier flowering corresponds to faster growth, which agrees with findings by Flory et al. (2011a, b). However, as an annual plant, *M. vimineum*'s success depends on seed production. The positive correlation between growth and fecundity in *M. vimineum* (Cheplick 2008, Warren et al. 2011b) suggests that US populations' faster growth represents increased fitness. However, a comparison of total seed output is necessary to confirm that the quicker growth of US genotypes results in greater fecundity than Asian genotypes.

Another explanation for the faster growth and earlier flowering in US *Microstegium* may be that the overall higher latitude and shorter growing season of the introduced range resulted in selection for genotypes that grow faster and flower earlier to maximize reproductive output prior to the end of the growing season. This quicker growth may have evolved at the expense of leaf structural traits, such as leaf toughness and SLA; previous studies have shown that faster growth is positively correlated to SLA and negatively correlated to leaf toughness (Krischik & Denno 1990, Grotkopp et al. 2002). Weber and Schmid (1998) suggested that adaptive evolution was responsible for the flowering times of two invasive *Solidago* species' following latitudinal gradients similar to the gradients of their native ranges. A significant positive correlation was observed between the latitudes of Asian and US populations collectively and percent of flowering individuals. But this correlation would also be expected between populations within each continent if flowering time is dependent on latitude. While a trend was found for flowering time along a latitudinal gradient for US populations, the relationship between flowering and latitude was very weak in Asian populations. This weak association among Asian populations may result from the zero-inflation caused by the absence of flowering in six of the ten populations, skewing the regression slope towards zero and decreasing the correlation coefficient. The lack of significant correlations within each continent may also be due to a low sample size (10 populations per continent). To determine if flowering time is associated with latitude, a larger number of populations from both continents should be assessed, allowing each population to flower prior to harvest.

Biomass measurements were not included in the data analysis because many individuals lost biomass through dropped seeds and leaf senescence. Harvest was planned to take place at the beginning of seed production but prior to seed dropping to prevent introduction of novel genotypes to study sites. Unfortunately, study plants set seed earlier than expected and at the time of harvest many US individuals (as well as some Asian plants) had already dropped seeds (common garden sites were subsequently sprayed with a grass-specific herbicide to prevent germination of dropped seeds). The designated harvest date corresponded to the phenology of naturally-growing *M. vimineum* populations adjacent to study sites, suggesting that early seed production was a response to the study plants’ unique growing conditions, specifically germination and seedling growth under the controlled conditions of a greenhouse.

Influences of site and population

The random effects of site and population were important parameters in models of leaf toughness, SLA, leaf damage, and flower production. The importance of population in models to describe the genotypic variability among included populations had a measurable influence on plant trait variation. The inclusion of site in top models reflects the plastic response of *M. vimineum* to the differing environmental conditions at study sites; phenotypic plasticity in *M. vimineum* is well-documented (reviewed by Warren et al. 2010; Flory et al. 2011a, b). The inclusion of population by site interactions in top models of SLA and leaf toughness indicates that the extent of the plants’ plastic response to environmental conditions depended on the population they came from. However, SLA was never higher and leaf toughness was never lower for Asian plants at a particular site indicating that environmental conditions influence differences in leaf structural traits between populations (i.e. genotype by environment interactions) but not to the extent of inverting the direction of these trait differences between US and Asian genotypes. While top models for flower production, SLA, and leaf damage only included origin as a fixed effect, the fixed effect for the best leaf toughness models was the three-way interaction between origin, soil moisture, and diffuse light. The importance of soil moisture, light availability, and their interactions with origin for leaf toughness variation offers further evidence that differences between genotypes are related to environmental conditions. The difference in fixed effects included in top models for leaf toughness relative to top models for other dependent variables may result from leaf toughness measurements taken during the growing season, while flower production, SLA, and leaf damage were measured on harvested plants.

Genetic variance

Genetic variance among an introduced species is necessary for adaptive evolution to occur (Bossdorf et al. 2005). If the Asian populations do, in fact, represent a variety of genotypes from the native range, which is highly likely given the geographic distance among source populations, then the greater variance in SLA and leaf damage in US populations and similar variance in leaf toughness between Asian and US genotypes suggest that there is substantial genetic variance in the introduced range. Substantial genetic variance indicates that *M. vimineum* was introduced on multiple occasions and that differentiation in the introduced range is not a result of a genetic bottleneck or founder effect (Bossdorf et al. 2005). Genetic variance can be further evaluated through comparisons of populations' neutral genetic variation using molecular markers (Bossdorf et al. 2005).

Evaluating genetic differentiation and the EICA hypothesis

Several criteria are required to evidence the EICA hypothesis. Tests of the EICA hypothesis should include multiple common gardens in both the native and introduced ranges (Hierro et al. 2005). If genotypes are compared in only one common garden and/or in only one of the ranges, differences in performance may be influenced by the environmental conditions of that particular site (i.e. genotype by environment interactions). Performing cross-continental common garden experiments also allows for a test of enemy release, which is a prerequisite of the EICA hypothesis. Evidence for enemy release would be provided by lower damage on all genotypes in the introduced range relative to the native range (Keane and Crawley 2002).

Progeny of a large number of populations spanning both geographic ranges should be included in tests of the EICA hypothesis to capture substantial genetic variation in native and invasive ranges (Bossdorf et al. 2005, Hierro et al. 2005). However, if the native range source of introduced genotypes is known, only progeny of the source population need to be included (Siemann and Rogers 2003a, Bossdorf et al. 2005).

Genetic variance upon which selection can act is necessary for EICA, as the acquisition of beneficial traits by mutation would require much more time (Lee 2002, Bossdorf et al. 2005). Processes other than EICA that can result in genetic differentiation and that also require substantial genetic variance in introduced populations include intraspecific and interspecific hybridization (reviewed by Lee 2002) and evolution of increased plasticity (reviewed by Richards et al. 2006).

Few studies have fully tested the EICA hypothesis by comparing native and invasive genotypes in both ranges because of the logistic and financial challenges. However, a common garden study by Zou et al. (2008) on the Asian tree *Sapium sebiferum* in its native range followed common garden experiments performed by Siemann and Rogers (2001, 2003a, b) in the continental US where *S. sebiferum* is invasive (also see Blaire and Wolfe (2004) and Wolfe et al. (2004) for cross-continental studies on *Silene latifolia*). Zou et al. (2008) found that herbivore damage, tolerance, and competitive ability of *S. sebiferum* were greater in introduced genotypes in the native range. In invasive range studies, reduced resistance and greater vigor were observed in introduced *S. sebiferum* and herbivore damage was similarly low on all genotypes (Siemann and Rogers 2001, 2003a, b).

The results of these cross-continental studies on *S. sebiferum* appear to support predictions of the EICA hypothesis. However, determination of whether or not EICA contributed to invasion by *S. sebiferum* is compromised by comparisons of genotypes in only single common gardens per continent (Siemann and Rogers 2001, 2003a, b; Zou et al. 2008) and including genotypes from only a few populations from either origin (Siemann and Rogers 2001, 2003a, b).

Genetic differentiation in *M. vimineum*

US *M. vimineum* populations' greater leaf damage, earlier flowering, and substantial variance in leaf toughness, SLA, and leaf damage appear to support the EICA hypothesis. The lag in identification of *M. vimineum* as an invasive species (Barden 1987) subsequent to its first US identification in 1919 (Fairbrothers and Gray 1972) further supports EICA because sufficient evolutionary time would have been required for selection to act upon *M. vimineum*'s genetic variation and result in evolution of decreased resistance and increased vigor (Bossdorf et al. 2005).

Genetic differentiation and invasiveness of *M. vimineum* in the US may be attributed to processes other than, or in addition to, EICA, such as evolution of increased plasticity or hybridization. However, Flory et al. (2011a, b) found no difference in phenotypic plasticity between Asian and US *M. vimineum*, indicating that evolution of greater plasticity did not contribute to invasiveness. While 13 species of *Microstegium* have been documented in China (Chen and Phillips 2007), no congeners of *M. vimineum* occur in the US (Flory et al. 2011b), negating the possibility of interspecific hybridization as a cause of genetic differentiation. However, *M. vimineum* genotypes that were isolated in the native range may have traded genetic material in the introduced range; novel genetic exchanges increase genetic variability and have been observed to enhance performance in other introduced species (reviewed in Lee 2002).

To further assess the viability of the EICA hypothesis for *M. vimineum*, a study of genetic differentiation needs to be completed in the native range (Hierro et al. 2005). A reciprocal experiment in Asia would test if performance differences observed in the US were influenced by environmental conditions of the introduced range. In the US, Flory et al. (2011b) found no influence of *M. vimineum*'s seed origin on the relationship between growth and environmental parameters across 22 common gardens, suggesting genotype by environment interactions did not play a role in US *M. vimineum*'s greater growth. Additionally, comparison of enemy damage between the native and introduced ranges would test for enemy release, which is required for EICA to occur.

Aside from a native range experiment, exploration of several other aspects of this system could provide further insight into whether or not EICA contributes to the invasiveness of *M. vimineum*. Maternal effects may have contributed to differences between populations in this study. To eliminate maternal effects, *M. vimineum* populations could be grown in a greenhouse and allowed to reproduce; cross-pollination should be prevented so that seeds maintain the genetic identities of parent plants. The progeny could then be assessed for genetic differences without the influence of variable maternal environments (Hierro et al. 2005). Additionally, other resistance traits, such as silica concentration, should be compared between US and Asian genotypes to directly evaluate if the greater enemy susceptibility of US populations results from reduced defense investment.

Conclusion

The greater growth, earlier flowering, and higher enemy damage in US populations offer evidence for EICA as an explanation for *M. vimineum*'s invasiveness. However, intraspecific hybridization may have also contributed to invasiveness by increasing genetic variance in introduced populations. A common garden experiment must be conducted in the native range to test if differences in performance were due to environmental conditions of the introduced range. Also, a comparison of enemy damage between native and introduced ranges would allow for assessment of enemy release.

Understanding how non-native plants invade improves land managers' ability to control the spread and prevent establishment of invasives. If EICA is a prominent invasion mechanism, stronger emphasis should be placed on early detection and identification of potential invaders; doing so will prevent adaptation to the introduced habitat, which may result in evolution of invasiveness. To control and eradicate exotic plants that have already invaded, such as *M. vimineum*, vulnerable life stages should be identified through studies of demographic-specific niche requirements.

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