A comparison of *Miscanthus sinensis* and two native grasses in their resistance and tolerance to herbivory by a generalist insect

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Abstract

Understanding how exotic species become invasive and how they interact with native plants and animals in the introduced range has economical, agricultural, medical and ecological importance. One of the possible mechanisms which allow the successful spread of exotic plant species is plants' release from their native specialist herbivores (Fig.1) and reallocating their resources towards growth and reproduction in the introduced range (Blossey & Notzold, 1995). This hypothesis, however, received mixed support in experimental studies, and many authors emphasize that future studies need to focus on plant responses to generalist herbivores (e.g. Bossdorf et al., 2004), as well as on simultaneous obtaining combined data on multiple traits in the same plant species (Atwood & Meyerson, 2011). Based on these ideas, we studied both tolerant and resistant responses of an exotic potentially invasive *Miscanthus sinensis* ('*Zebrinus*' and '*Gracillimus*' cultivars) and two native grasses, *Andropogon gerardii* and *Bouteloua curtipendula*, to herbivory by a generalist insect, the grasshoppers of the *Melanoplus* genus. Results of feeding experiments using nymph grasshoppers demonstrated significantly lower resistance of *M. sinensis plants* than that of native grasses and no significant difference in tolerance to herbivory between native and exotic group of plants.

Specific Aims and Hypotheses

In this study we focused on two research questions: (1) Do native and exotic plants differ in their tolerance to herbivory?, and (2) Do native and exotic plants differ in their resistance to herbivory?

We hypothesize that if the assumption about reallocating resources by invasive plants is met, exotic plant species in our study will demonstrate higher tolerance (***Hypothesis 1***) and lower resistance (***Hypothesis 2***) to native generalist herbivores than native plants.

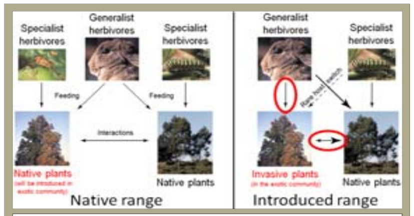

Figure 1. Enemy release in a simplified community; interactions between herbivores and plants (black arrows) in native community and in the exotic community containing invasive plant species (modified from Keane & Crawley, 2002). Bold arrows represent a greater impact of generalist herbivores on native plants and, as a result, outcompetition of native plants by invasive plants. Red circles represent the focus of the presented study.

Materials and Methods

Study Organisms

Andropogon gerardii

Bouteloua curtipendula

Miscanthus sinensis 'Zebrinus'

Miscanthus sinensis 'Gracillimus'

Feeding Experiments

Plants were obtained from plant nurseries and planted in the field in two "native-exotic" pair combinations: *A. gerardii/ M. sinensis 'Zebrinus'*, and *B. curtipendula/M. sinensis 'Gracillimus'.* For each plant combination, six open air aluminum screen cages (16×16×20") were set up and divided by a window screen, separating plant pairs with and without exposure to grasshoppers (Fig.2). Two grasshopper nymphs were placed in each cage for five days.

Nymph *Melanoplus sp.*

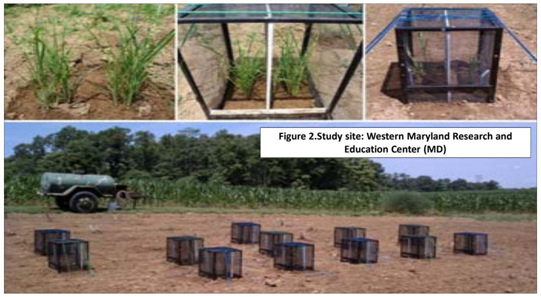

Figure 2.Study site: Western Maryland Research and Education Center (MD)

Materials and Methods (cont.)

Measurements

To estimate plant tolerance , we determined the growth rate of plants using multiple measurements: the length of their longest leaf (Fig.3), the number of leaves (Fig.4) , and a proxy of biomass, 'height × number of leaves', at the beginning and at the conclusion of the experiments [(day 5 measurement - day 0 measurement) / day 0 measurement].

Figure 3. Measuring height of plant as the length of the longest leaf.

Figure 4. Measuring the number of leaves.

To estimate plant resistance , we quantified the volume of the grazed portion from the leaf tissue (length × width × depth of scars, mm^3) and frequency of scars left by grasshoppers (number of scars/number of leaves) (Fig. 5, 6).

Figure 5. Scar – a leaf portion, grazed by grasshopper.

Figure 6. Measuring the volume of grazed portion.

Data Analysis

This proxy of biomass, "height × number of leaves", was chosen using general linear model (GLM); it explained a significant amount in biomass variation for all plant species (P<0.05), except *M. sinensis 'Zebrinus'* (P>0.05)(Table1). The highest correlation coefficient [0.86] was observed for *A.gerardii* plants (Fig.7).

Table 1. GLM summary.

Plant species	Null deviance	Residual deviance	*P*-value
M. sinensis 'Zebrinus'	39.308	37.807	0.5428
M. sinensis ''Gracillimus'	21.794	13.344	0.0306
A. gerardii	355.717	86.816	0.0002
B. curtipendula	38.5630	9.7068	0.0003

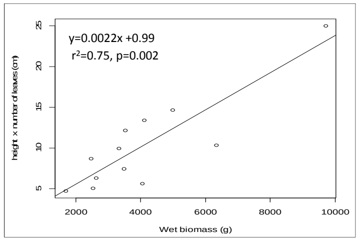

Figure 7. Relationship between wet biomass and the product of height and number of leaves in *A. gerardii* plants.

Grasshopper nymph feeding on a leaf

Plant tolerance and plant resistance between native and invasive plants were compared relatively to control plants, using a two-way nested ANOVA. All data analysis was conducted in R (v.2.15.2).

Results

Plant Tolerance

Growth rate based on height and the biomass proxy, "(height) x (number of leaves)", did not differ between exotic (*M. sinensis 'Zebrinus,' M. sinensis 'Gracillimus'*) and native (*A. gerardii*, *B. curtipendula*) groups of plants (Height: $F_{1,6}$= 0.34, P= 0.58; [height x number of leaves]: $F_{1,10}$= 0.79, P= 0.34) (Fig. 8,9).

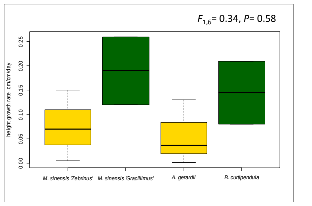

Figure 8. Mean differences in height growth between plants. Exotic plants did not significantly differ in height growth from that in native plants (P>0.05).

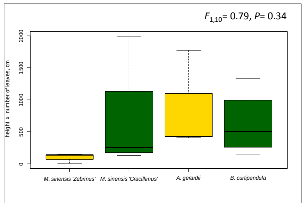

Figure 9. Mean differences in a proxy of biomass, "height × number of leaves", between plants. There was no significant difference in this measurement between plants (P>0.05).

Plant Resistance

The volume of the grazed portion, number of scars, and frequency of "scarring" were greater in exotic (*M. sinensis 'Zebrinus,' M. sinensis 'Gracillimus'*) plants than in native (*A. gerardii*, *B. curtipendula*) plants (Volume of grazed portion: $F_{1,20}$= 10.64, P= 0.004; Frequency of "scarring": $F_{1,20}$= 6.06, P= 0.023) (Fig. 10,11).

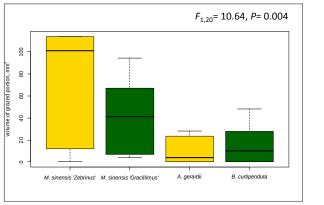

Figure 10. Mean differences in volume of grazed portion between plants. Exotic plants demonstrated significantly greater leaf damage than native plants (P<0.05).

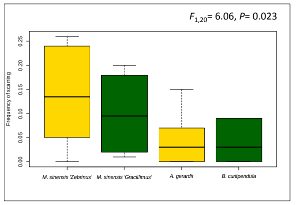

Figure 11. Mean differences in frequency of "scarring" between plants. Exotic plants demonstrated significantly greater frequency of "scarring" than native plants (P<0.05).

Discussion

Our results did not support Hypothesis 1, which stated that exotic plants would have higher tolerance to herbivory than native plants. Plant tolerance did not differ between native plants (*A. gerardii*, *B. curtipendula*) and exotic *M. sinensis* plants (*'Zebrinus' and 'Gracillimus'* cultivars). Our results suggest that, having the same effect from feeding by grasshoppers, exotic *M. sinensis* plants tolerate herbivory as effectively as native plants.

We also found that the product of height and number of leaves in these grasses can be successfully used for our future studies as a proxy of biomass, specifically for comparing growth rate between different plant species.

We found lower resistance to herbivory in exotic *M. sinensis* plants compared to that of native plants; therefore Hypothesis 2 was supported in this study. Lower resistance of *M. sinensis* can be explained by the fact that exotic species do not co-occur with the grasshoppers of the *Melanoplus* genus in the native range, and therefore might be less defended against these herbivores. In addition, feeding preferences of grasshoppers towards novel food, such as these exotic plants (Bernays & Chapman, 1994) might also affect the leaf damage data.

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