Competition and herbivory in co-invasive, non-native plants of the suburban/exurban forest herb layer

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Introduction

Suburban/exurban forests are often invaded by multiple, non-native plant species. When these plants become dominant, their competitive interactions with each other and their interactions with herbivores and pathogens may become important drivers of community dynamics - including the ultimate competitive success of the different co-invasive species. Most research, however, focuses on invasive species' competition with native species, and it often is assumed that invasive plants have escaped significant enemy attack.

We conducted a field experiment to investigate whether three co-invasive species of the temperate deciduous forest herb layer did indeed escape natural enemies, and if they differed. We compared a biennial forb, garlic mustard (*Alliaria petiolata*, ALPE), an annual grass, Japanese stilt-grass (*Microstegium vimineum*, MIVI), and a tree seedling, Norway maple (*Acer platanoides*, ACPL).

We also tested the combined effects of competition and herbivory on ALPE and MIVI in the greenhouse. We used a response surface design that varied both plant density and the frequencies of the two species, for differing levels of intraspecific and interspecific competition, and we included the interaction of competition with simulated deer browsing, using clipping treatments. Invasive plants typically are thought not to be subject to deer browse, but in denuded forests where invasives become dominant, that can change. The future community structure may then depend not only on competitive interactions between co-invasive species, but also on their relative tolerance of herbivory.

Alliaria petiolata

Microstegium vimineum

Acer platanoides

Figure 1. Leaf damage on three invasive plant species, observed in the field experiment.

Methods

FIELD EXPERIMENT

- Started seedlings in The College of New Jersey greenhouse of four species [*Alliaria petiolata* (ALPE), *Microstegium vimineum* (MIVI), *Acer platanoides* (ACPL), and a native neighbor, *Acer saccharum* (ACSA)], from locally collected seed.
- In May, planted seedlings into individual 1-m^2 cleared plots within three forests in central New Jersey: Mercer County Park Northwest (MCP), Washington Crossing State Park (WCR), and Stony Brook/Millstone Watershed (WSHD); watered until established.
- Planted a total of 120 focal seedlings, assigned to one of four treatments: focal species 1) alone; 2/3) with two seedlings of one of the other invasive species; or 4) with two individuals of the native ACSA.
- Harvested the surviving focal plants in September; scanned fresh leaves (Fig. 1); analyzed digitally for herbivory and necrosis (disease proxy) using CIAS 2.0.

GREENHOUSE EXPERIMENT

- Cold/moist stratified locally collected seeds of ALPE and MIVI; planted in flats.
- Transplanted seedlings to pots as in Fig. 2.
- 12 density X frequency treatments; 4 replicates each in 3 blocks (12 total per treatment combination).
- Grew for 2 months; harvested whole plants; separated roots and shoots of each species; oven dried at 60C.
- Recorded dry mass of roots and shoots of each species from each pot; divided by number per pot for per capita mass per pot.

Figure 2. Response surface planting design used in the greenhouse experiment. It crossed ALPE:MIVI species frequencies of 20:80%, 40:60%, 60:40% and 80:20% with pot densities of 5, 10, or 20 plants.

Density	Percent ALPE to MIVI			
	20/80	40/60	60/40	80/20
5	M M A M M	A M M M A	M A A A M	A A M A A
10	M M M M A A M M M M	M A A M M M A A M	A M M A A A M M A	A A A A M M A A A A
20	M M M M A M A M M M M M M M A M A M M M	M A M M A M A M A M M A M A M A M M A M	A M A A M A M A M A A M A M A M A A M A	A A A A M A M A A A A A A A M A M A A A A

Results – FIELD EXPERIMENT

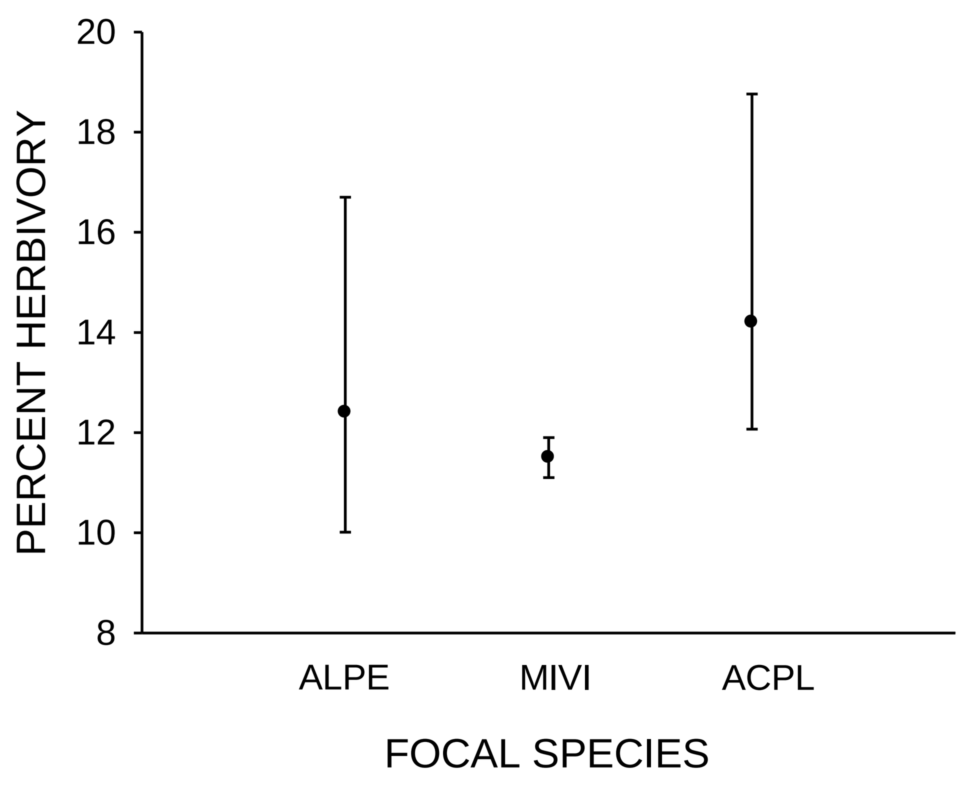

Figure 3. Percent leaf area with herbivory for all three species was very similar, with the highest value approximately 15% (the presence of competitors was not influential, so the data were pooled across competitor treatments).

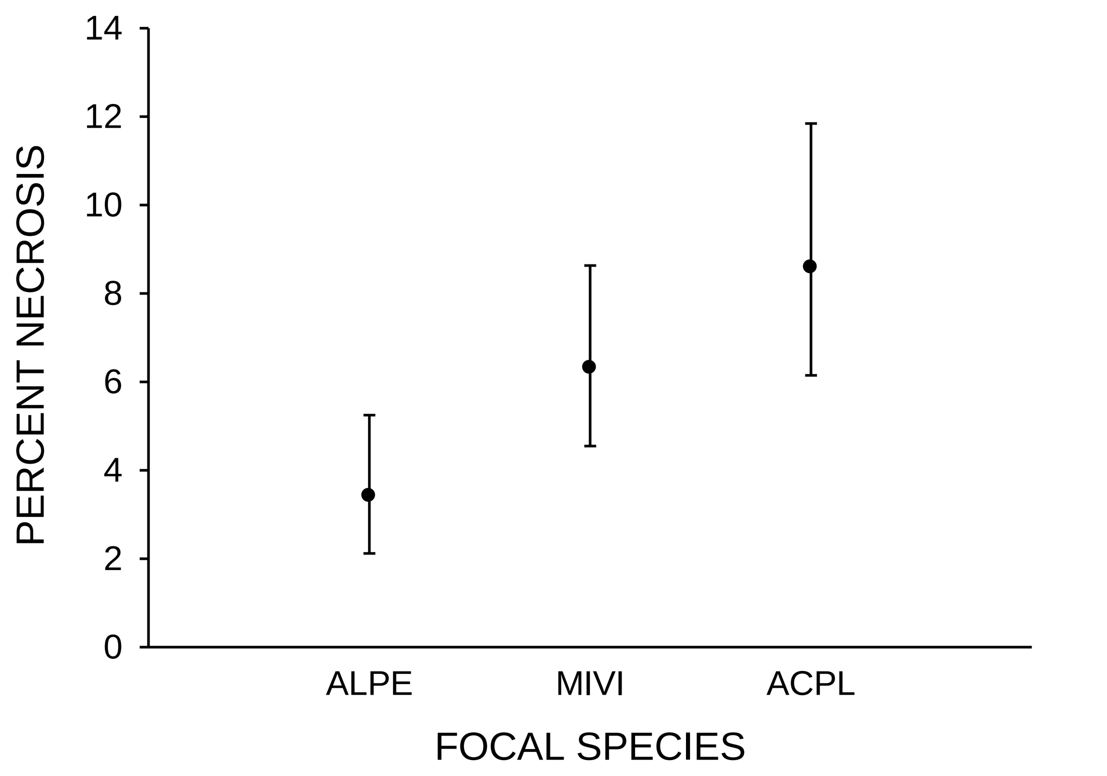

Figure 4. ALPE had the lowest percent leaf area with necrosis (disease proxy), approximately 3.5%, about half as much as the necrosis of MIVI (6.3%) and ACPL (8.6%) (ACPL competitors were removed from the ALPE and the MIVI data, see Figs. 5 & 6).

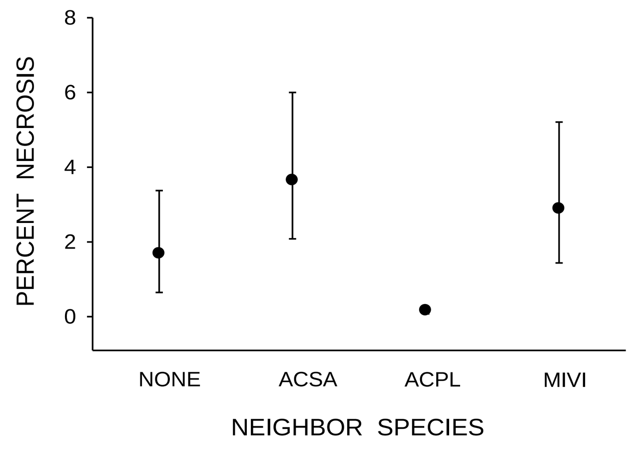

Figure 5. Percent necrosis of ALPE growing with ACPL as a neighbor decreased by an order of magnitude (to 0.17%) in comparison to its growth with other species as neighbors.

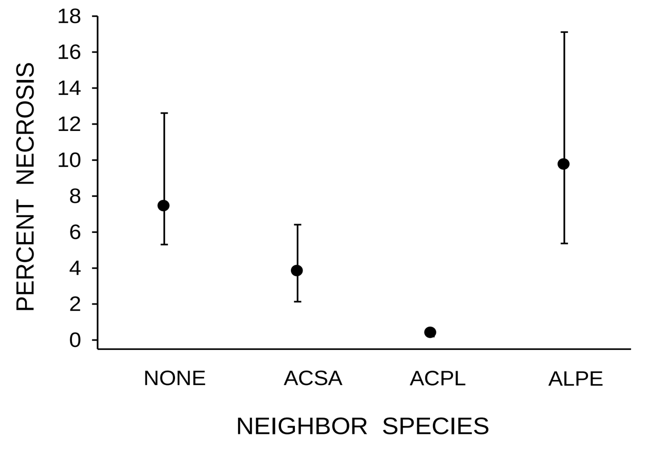

Figure 6. Percent necrosis of MIVI growing with ACPL as a neighbor decreased by an order of magnitude (to 0.39%) in comparison its growth with other species as neighbors.

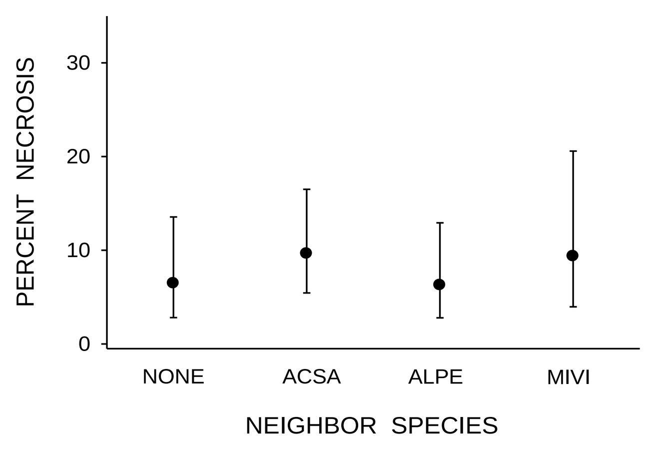

Figure 7. The neighboring species had similar effects on the percent necrosis of ACPL.

Results – GREENHOUSE EXPERIMENT

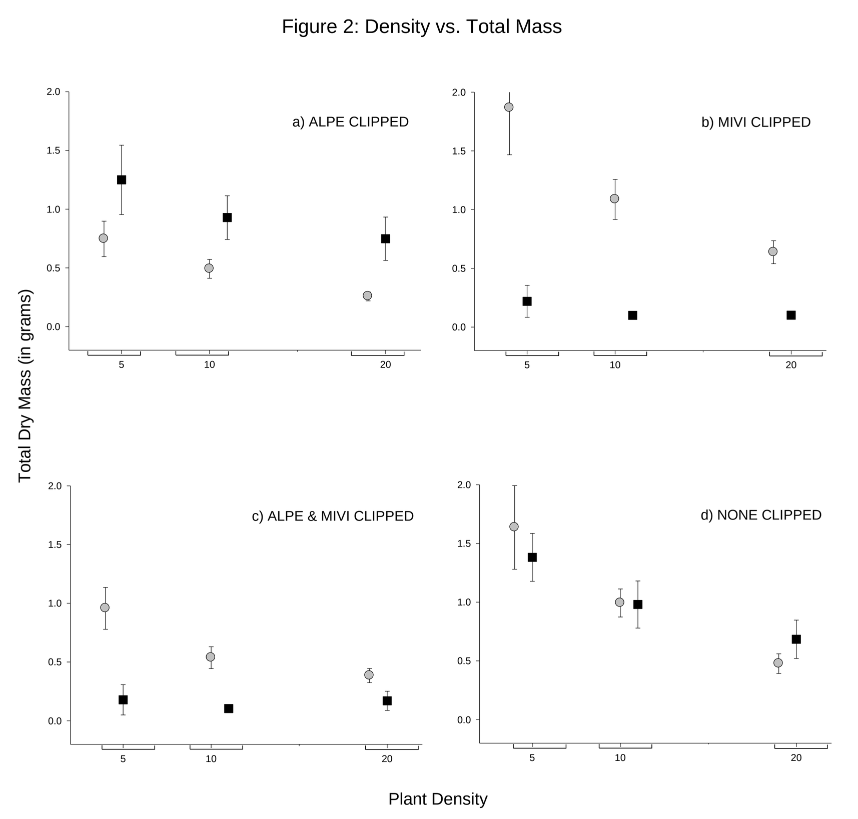

Figure 8. Both ALPE and MIVI grew smaller as competition from other plants increased (density), under all clipping treatments ("herbivory"). Without clipping, they both grew to similar mass. When ALPE was clipped, ALPE plants experienced a 50-60% reduction in mass, and MIVI plants were unaffected. When MIVI was clipped, MIVI mass was reduced by 75-85%, and ALPE mass increased by 15-25%.

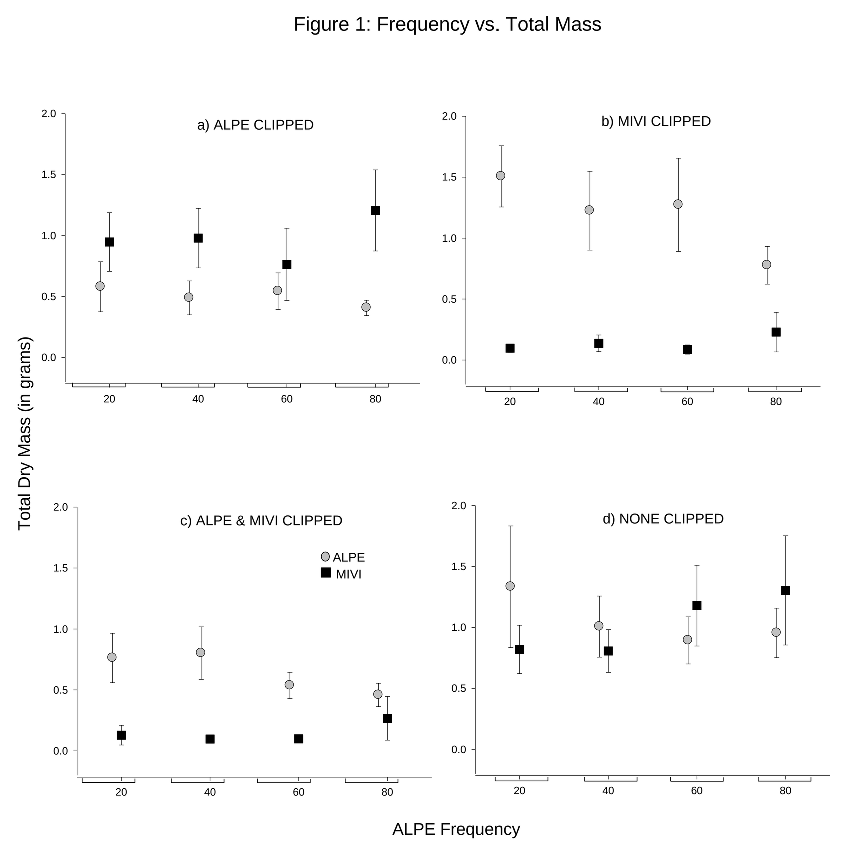

Figure 9. Intraspecific vs. interspecific competition (frequency) had weaker and more complex effects on plant growth, compared to density. With no clipping or when just ALPE was clipped, plants tended to grow smaller with greater intraspecific competition. This effect was more pronounced for MIVI than ALPE. When MIVI was clipped, the intraspecific competitive effect among ALPE plants increased and among MIVI decreased.

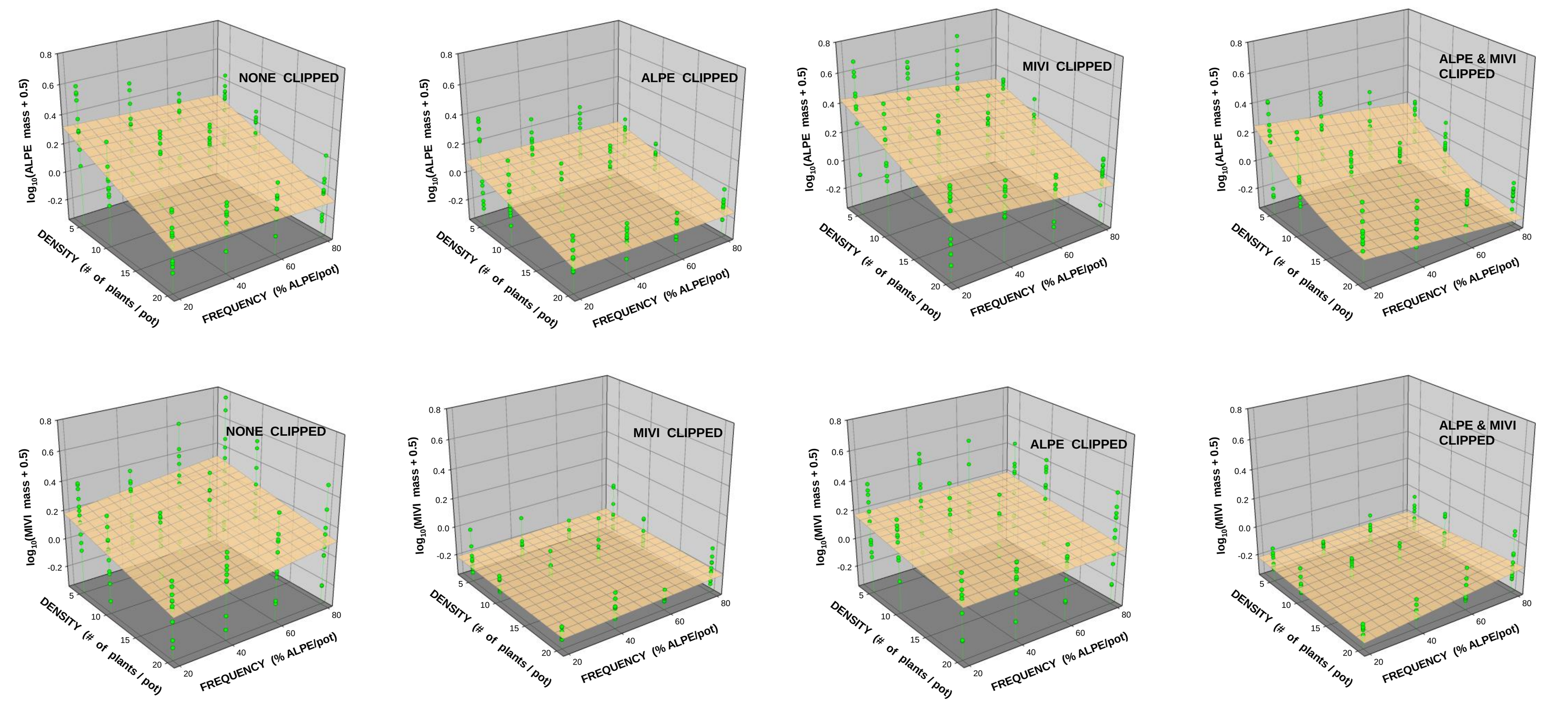

Figure 10. The combination of density and frequency effects allowed for construction of response surface regression models for each species, which were much more predictive for ALPE than MIVI. The simulated herbivory treatments affected the surfaces mostly through the magnitude of the responses. The shape of the response was altered in some cases: clipping of either or both species removed the negative response of MIVI to increased intraspecific competition; for ALPE, clipping of MIVI or both revealed a negative response to increased intraspecific competition.

	EFFECTS AND SIGNIFICANCE OF REGRESSION TERMS					
	DENSITY	FREQUENCY (% ALPE)	$DENS^2$	$FREQ^2$	DENS*FREQ	R^2
ALPE						
NO CLIP	*** (-)	ns	ns	ns	ns	0.39
ALPE CLIP	*** (-)	ns	ns	ns	ns	0.29
MIVI CLIP	*** (-)	*** (-)	ns	ns	ns	0.37
BOTH CLIP	*** (-)	*** (-)	** (+)	ns	ns	0.33
MIVI						
NO CLIP	*** (-)	* (+)	ns	ns	ns	0.12
MIVI CLIP	ns	ns	ns	ns	ns	0.03
ALPE CLIP	** (-)	ns	ns	ns	ns	0.06
BOTH CLIP	0.09 (-)	ns	ns	ns	* (+)	0.10

Discussion

Many suburban/exurban forests have few native plant species and are increasingly dominated by non-native, invasive plants. Interactions among these species and the ubiquitous deer may become driving forces in the future structure of these communities.

This study revealed that herbivory and disease symptoms were present and substantial for all three non-native invasive plant species, contrary to the Enemy Release Hypothesis, which predicts that non-native species that become invasive have escaped their natural enemies. We also observed a strong indirect effect between certain invasive-invasive neighbor pairs. The presence of Norway maple (*Acer platanoides*, ACPL) dramatically mitigated the cause(s) of leaf necrosis in both garlic mustard (*Alliaria petiolata*, ALPE) and Japanese stilt-grass (*Microstegium vimineum*, MIVI). Such a protective effect of one invasive species on others could lead to facilitation of the protected species' invasions. Further study is warranted to determine the mechanism of this facilitative effect and whether it could provide a window of opportunity for colonization, or even could lead to invasional meltdown.

Our comparison of necrotic symptoms among the three species showed that ALPE experienced less leaf tissue loss than the other species. Assuming that this correlates to greater photosynthetic capacity, such variability in susceptibility would provide an advantage to ALPE in communities undergoing co-invasions by these species.

The greenhouse experiment provided evidence for the possible outcome of competitive interactions between ALPE and MIVI in deer-impacted forests. With no herbivory (clipping), the species with lower intraspecific competition outgrew the other, except at the highest density, when MIVI always outgrew ALPE. When just one species was clipped, it was outgrown by the other species at all densities and ALPE:MIVI ratios. When both were clipped, ALPE outgrew MIVI in all cases, because clipping was much more detrimental to MIVI than ALPE. The implications for natural communities are that ALPE should be able to invade MIVI stands and vice versa at lower densities, but when the invasion(s) result in high densities, MIVI should dominate – unless deer herbivory on these species is a factor. In that case, the relative deer impact on the two species will determine their competitive outcome.

***Alliaria petiolata* (top) and *Microstegium vimineum* (bottom) growing intermingled in the forest herb layer .**

Acknowledgements : Many thanks to Brian Dunn and Kelly-Marie McCartney for planting, harvesting and scanning plants in the field experiment; to Stony Brook Millstone Watershed Association, Mercer County Dept. of Parks, and Washington Crossing State Park for research permits; to David Melman, Scott Morrison Melman, Jason Wong, and Jen Aleman for help harvesting plants in the greenhouse; to TCNJ Academic Affairs and the SOSA Committee for reassigned time for research to J. Morrison and support for the Biology Summer Research Program and the Mentored Undergraduate Summer Experience; to the Dept. of Biology and School of Science for financial support.