

Spatial and Temporal Dependent Shifts in Grassland Invasibility

by

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Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the

Biology

Program

YOUNGSTOWN STATE UNIVERSITY

July 28, 2010

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Abstract

A biological community can become invaded by non-resident species when the resources necessary for establishment and growth coincide with invader propagules. There are many ecological factors that affect below- and aboveground resource availability in a community and this research integrates both spatially and temporally varying components. In a managed grassland, we measured the interactive effects of disturbance patch size (DPS), grazing intensity (GI), and soil resource availability (SRA) on the invasion success of smooth pigweed *Amaranthus hybridus* (L.) and velvetleaf *Abutilon theophrasti* (L.). Importantly, we considered two life history stages of each focal invader (i.e., emerged and established seedlings) because invasion success may depend on when resource shifts coincide with particular life history stages. Our empirical data generally support the following predictions: 1) thresholds in ISP exist across DPS, the magnitude of which increases with higher SRA levels, 2) the life history stage of the invader strongly affects ISP in smaller sized patches containing high SRA, 3) regardless of invader size, grazing effects are large in small DPSs in high SRA area 4), in the absence of grazing, SRA within a given DPS can have opposing effects on ISP. Integrating disturbance type and intensity across other ecological dimensions is important in elucidating the mechanisms of community invasibility as well as offering sound recommendations to managers of native grassland communities.

Acknowledgements

Thank you to Rick Relyea and the Pymatuning Laboratory of Ecology for the use of their field and facilities, making my research possible.

I am grateful to Dr. Renne for his guidance, patience, and for helping me to become more independent by giving me a project that challenge me and pushed me out of my comfort zone.

I would like to thank Dr. Diggins and Dr. Armstrong for all their help as committee members. I would especially like to thank Dr. Diggins for being a mentor to me and always believing in me over the last 8 years. He opened up many research opportunities for me, making it possible for me to grow as a scientist, and I will never forget that.

I'm extremely grateful to Dr. Andy Chang for all of his guidance and patience in helping me with my data analysis. His time and effort on my behalf are largely responsible for me graduating this summer.

I would like to thank Brandon Sinn, Jacob Saborse, and Bruce Cicone for all of their hard work out the field. We could not have pulled it off without you!

I would like to thank my family for always believing in me, putting up with me, and especially for my parents pushing me at a young age. Finally, I would like to thank my husband for always standing by me, no matter how insufferable I could be.

Table of Contents

Abstract.....	i
Acknowledgements.....	ii
Table of Contents.....	iii
List of Figures.....	iii
List of Tables.....	iv
Introduction.....	1
Methods.....	7
Results.....	14
Discussion.....	25
References.....	32

List of Figures

Figure 1. Study site and experimental design	8
Figure 2. <i>A. theophrasti</i> means.....	15
Figure 3. <i>A. hybridus</i> means.....	16
Figure 4. ABTS quantile plot low GI.....	18
Figure 5. ABTS quantile plot High GI.....	18
Figure 6. AHTS quantile plot low GI.....	20
Figure 7. AHTS quantile plot High GI.....	20
Figure 8. ABES quantile plot low GI.....	21
Figure 9. ABES quantile plot high GI.....	22

Figure 10. AHES Tobit plot.....	22
Figure 11. PARss Means.....	23
Figure 12. PARss Quantile Plots.....	23

List of Tables

Table 1. ABTS quantile regression results.....	19
Table 2. AHTS quantile regression results.....	20
Table 3. ABES quantile regression results.....	21
Table 4. AHES quantile regression results.....	22
Table 5. ABES seedling results.....	23
Table 6. AHES seedling results.....	23
Table 7. PARss quantile regression results.....	24

Introduction

Elucidating mechanisms of plant community invasibility involves understanding how interactions between residents and the physical environment affect resource availability and importantly, how variability in a few key factors can significantly affect state changes in invasibility. Invaders are capable of greatly altering ecosystem structure and function and pose a considerable threat to biodiversity (Lonsdale 1999). The ever increasing negative economical and ecological consequences of plant community invasions have prompted much investigation into the phenomenon. Invasibility is defined as the vulnerability of a community to establishment and growth by non-residents (Davis 2005). However, it is not necessarily the notion of invasibility itself that is in question, but the mechanisms behind it. Community composition and invasibility are determined by complex biotic and abiotic processes which operate and interact at multiple spatial and temporal scales (Huston 1979; Kumar et al. 2006; Renne 2006; Britton-Simmons and Abbott 2008). Many studies examine how interacting ecological forces affect resident diversity and the susceptibility of communities to invasion), and have found they are forces that alter the disturbance regimes and resources availability (Tilman 1993, Huston 2004, Burke and Grime 1996, Haddad 2008; Naeem et al. 2000; Fargione 2006; Davis 2000). For example, large mammalian herbivores can significantly alter nutrient cycling as well as soil disturbance and grazing regimes of grasslands (Hayes and Hall 2003), potentially increasing its susceptibility to invasion as well as altering the community's composition through strong top-down regulatory effects (McNaughton 1979).

Investigators have used niche-based theories to assess the contribution of individual species traits to invasion success in a community (Huston 2004, Gasso 2009) a collection of similar traits have emerged (Garnier et al. 2001; Milbau 2003; Fargione 2006). Despite this, the use of invader-specific traits has tended to be problematic in predicting invader success. Environmental conditions affecting resource availability may determine which particular traits are beneficial to a potential invader; e.g. low tissue nitrogen and high root: shoot ratio may be favored in N-limited environments (Vitousek 1982; Pennings et al. 2005; Fargione and Tilman 2006).

Another traditional approach to evaluating community invasibility has been to focus on characteristics of the recipient community. Resident diversity has historically been viewed as important to invasion resistance (Rejmanek and Richardson 1996; Tilman et al 1997; Lavorel et al. 1999; Stohlgren et al. 1999; Naeem et al. 2000). Elton (1958) proposed that low resident diversity and empty niches decreased invader resistance of a community, although recently the mechanisms underlying this hypothesis have come into question (Levine and D'Antonio 2000; Naeem et al. 2000). Tilman (2004) argues that high resource use efficiency in speciose communities generally lowers resources for establishment (Rejmanek 1996; Loreau 2000; Stohlgren et al. 2008) and other theoretical and empirical studies support this long held paradigm, although it appears observational studies do not (Stohlgren et al. 1999; Levine and Dantonio 1999; Naeem et al. 2000; Huston 2004). Naeem et al (2000) found that when factors which covary with diversity are removed (e.g., soil disturbance, grazing, resource fluxes), Elton's hypothesis is supported. However, biotic and abiotic covarying factors will often be present and the

nature of those factors can change the relationship between resident diversity and the invasibility of a community). The concept of functional diversity has recently been defined by Tilman (2001) as ‘the value and range of those species organismal traits that influence ecosystem function’. This definition describes a hypothesis based on species-specific traits, which has already shown to be an unreliable predictor. The concept of functional diversity has provided a greater understanding of the structural forces of plant communities but fails to reliably explain invasibility, particularly when multiple extrinsic covarying factors are simultaneously introduced, such as soil disturbance, grazing, and soil resource fluctuations. It is much more likely that resource availability changes spatially and temporally, due to such processes as fire, flood, and grazing (Stohlgren et al. 2008).

It is becoming clearer that invasibility is an important feature of a community, determined by biotic and abiotic factors that affect above and below-ground resource availability and many studies have found that fluctuations in these are drivers of biological community structure (Rajaniemi 2002; Bakker 2003; Henry et al. 2004; Houle 2005). Plants have relatively simple requirements for life; adequate sunlight, water, and nutrients. Due to the inverse relationship between soil resources and light availability, an increase in soil resources such as the addition of fertilizer, leads to increased above ground competition and consequently reduced propagule success (M. Henry, et al 2004; Pennings et al 2005). A large increase in productivity can reduce the spatio-temporal heterogeneity of limiting resources (Rajaniemi 2002), reducing or eliminating areas in which competition is low enough for successful recruitment (Hofman et al. 2004). The

productivity-diversity relationship (Rajaniemi 2002) is suggested to be unimodal - productivity will increase diversity to a point at which competitive exclusion occurs, after which diversity declines (Grime 1973; Houle 2005). However, the activity of grazers can shift the curve to the left or to the right, depending on productivity level of the community (Kondoh 2001, Osem 2002; Bakker 2003; Bakker 2006).

Soil disturbance exhibits the same unimodal relationship with diversity as productivity (Haddad 2008). The Intermediate Disturbance Hypothesis first postulated by Grime (1973), suggests that intermediate levels of disturbance prevent competitive exclusion (Takehiro et al. 2009). The prevention of competitive exclusion creates recruitment opportunities for fallen and buried seeds, as well as for lateral growth from the surrounding residents, the latter of which can be the most prevalent form of revegetation in grassland communities (Rogers and Hartnett 2001). Disturbance size is an important factor in what types of species colonize the patch. Generally, large disturbance patches can reduce establishment via desiccation or increased herbivory (Rogers and Harnett 2001) while the environment of a small patch may still be too competitive. However, in a study done by Thompson et al. (2001) the combination of additional nutrients and soil disturbance was found to increase invasibility more than if they had occurred separately. This relationship was further described by Huston (2004) who found through establishment probability, that communities were most invasible in low disturbance, nutrient poor conditions, as well as high disturbance nutrient rich conditions (Davis 2000; Renne et al 2006). Even though both sets of conditions make a community

more invulnerable, it is the latter set in which a potential invader is considered most likely to dominate and negatively impact a community (Huston 2004).

Exotic species may not be qualitatively different from resident species and the invasion of a plant community is facilitated by the same processes that affect resident diversity (Huston 1994; Kondoh 2001, Davis 2000). Past investigations have elucidated important interactions in an attempt to reveal mechanisms of invulnerability, but they failed to include several important factors. In this study we combine soil disturbance, grazing intensity and nutrient addition to assess their main and interactive effects on the invader success probability (ISP) of two species. The model organisms *Amaranthus hybridus* (L.) and *Abutilon theophrasti* (L.) produce very small and very large seeds respectively. Because of greater reserves, large seeds have a greater capacity than small seeds to withstand drought, shade, defoliation and competition and thus generally have higher invasion success probabilities (Moles et al. 2003; Moles and Westoby 2006; Herrera and Litter 2009). Being less susceptible to stress can increase the establishment potential of an individual by reducing the effect of microsite limitations.

Establishment is a critical juncture in the life of many plants and temporal fluctuations in below and above ground resources can determine invasion success (Tilman 2004; Renne 2006). The inclusion of life history stage into the study design allows for the examination of temporal resource fluctuations on community invulnerability. We also included as a temporal component, two different life history stages of each invader, in order to observe differences in treatment response. Young established

seedlings were used along with seedlings that emerged on site, to observe dissimilarities in ISP that may occur when environmental factors (e.g. grazing, soil disturbance, resource fluctuations) coincide with different life history stages.

Cattle grazing increases light availability by creating large canopy gaps and can increase productivity through substantial nutrient deposition, particularly nitrogen (Bakker 2003; Bakker). By preventing light competition and increasing spatio-temporal heterogeneity of resources, the activity of large mammalian grazers can potentially increase germination of propagules and establishment of resident and non-resident seedlings (Bakker 2006). Because grassland managers have control over some of these important ecological forces, they can effectively reduce the community invasibility of their system. The results of this study may have high applicability, by giving grasslands managers the ability to control invasion by undesirable species while maintaining high resident diversity.

This study assesses the interactive effects of soil resource availability (SRA), disturbance patch size (DPS), and grazing intensity (GI) on the invasibility of a managed grassland community and is an empirical test of invasibility models developed by Renne and Tracy (unpublished). We tested the following hypothesis: 1) thresholds in ISP exist across DPS, the magnitude of which increases with higher SRA levels, 2) the life history stage of the invader strongly affects ISP in smaller sized patches containing high SRA, 3) regardless of invader size, grazing effects are large in small DPSs in high SRA area and 4) in the absence of grazing, SRA within a given DPS can have opposing effects on ISP.

Because of its larger seed size, we also predict *A. theophrasti* (L.) will have a higher rate of establishment across all treatment combinations than *A. hybridus* (L.).

Methods

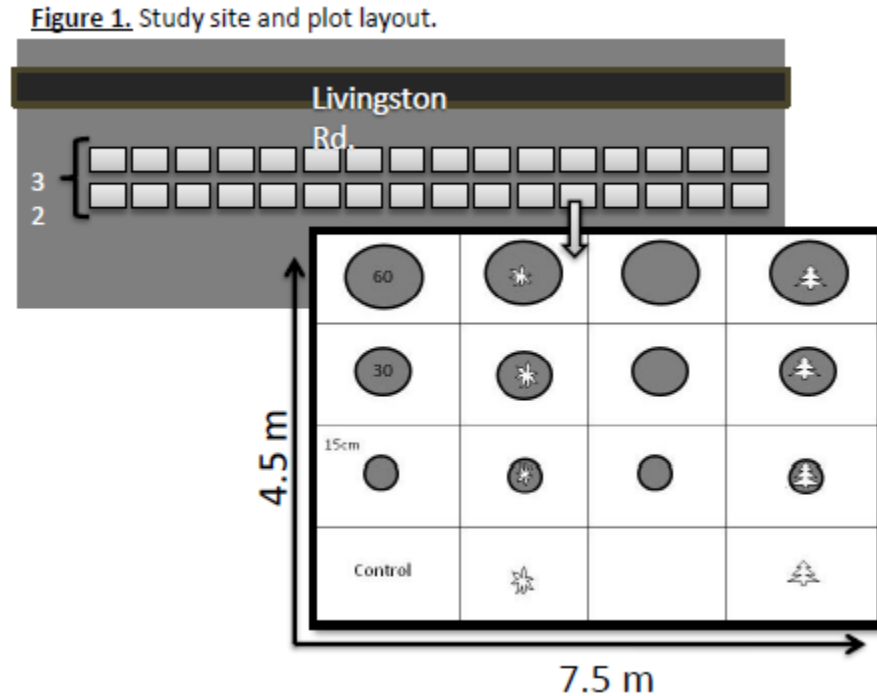
Study Site and Selected Species

This research occurred from late spring to early fall 2008 at the Pymatuning Laboratory of Ecology, University of Pittsburgh. A ten year old managed pasture was chosen that was relatively homogenous in moisture and species composition. Some of the dominant species present included orchard grass, tall fescue, white clover, and dandelion. Soil at the study site is poorly drained French Silt Loams (USSCS 1979) (Stevens et al. 2004).

Experimental Design

A completely random, balanced factorial, split-plot design was used to test two whole-plot effects of soil resource availability (SRA) (nitrogen; n=4) and grazing intensity (GI) (n=2), as well as the split-plot effect of disturbance patch size (DPS, n=4) (fig. 1). Due to the sedentary nature of plants, the neighborhood scale was considered suitable to observe the interaction of these three factors (Naeem et al. 2000). The site was divided into two transects of 16 plots (32 total), 7.5 x 4.5 meters in size with one meter separating each of the plots (figure 1). Each individual plot was further divided into 16

subplots (figure 1). The 32 plots were randomly assigned a combination of the first two factors, which resulted in four whole plot replicates of each treatment combination.



Two species were selected as model invaders; *Amaranthus hybridus* (L.) and *Abutilon theophrasti* (L.). *A. hybridus* is a small seeded native, while *A. theophrasti* is a large seeded non-native. Seed size was considered in the selection of the model species as it may be a factor in determining seedling success. Using Conetainers[®] that were six inches in length with a diameter of one inch, the transplanted seedlings (TS) were started 3 weeks prior to when they would be planted at the study site. The second life history stage of emerged seedlings (ES) was implemented by sowing approximately 15 seeds directly into the plots. Each of the 32 plots received eight transplanted seedlings (TS) of each species, within eight of the appropriate sub-plots. The remaining eight subplots received the ES for both species as well. The seeds and seedlings were placed in the

center of each of the sixteen subplots, which was also the center of each DPS if present (Figure 1).

SRA within the plots was manipulated using urea prepared in four concentrations of 0, 40, 100, and 250 kg N/ha. Urea dissolved in tap water was added as evenly as possible with watering cans over the entirety of each plot. GI was simulated using a conventional weed wacker by clipping the plots to a height of 12.5 centimeters, which was followed by a light raking to remove the clipped vegetation. This was done once in thirty days for the low GI plots in order to to simulate rotational grazing and twice in thirty days for the high GI plots to simulate over grazing. Each of the 16 subplots contained one of four disturbance treatments (figure 1). The four treatment levels consisted of a control of no disturbance, or a bare patch with a diameter of 15, 30, or 60 cm (figure 1). Soil with forage was removed from the 15 and 30 cm plots using a TurfMender (Par Aide, Lino Lakes, Minnesota, USA) to take out 15 cm plugs, six inches deep. A shovel was also used to remove the appropriate amount of soil from the 60 cm disturbance patches. Some of the soil removed was firmly packed back into the disturbance patch in order to create a divot that was approximately 2.5 cm in depth. Care was taken to ensure that no meristematic tissue was returned to the disturbance patches. The activity of cattle does not always result in the complete removal of vegetation, but may depending on cattle stocking rates, environmental conditions, and the species composition of the grassland itself (Renne et al 2006).

Data Collection

On 7-7-2008 and 7-23-2008, the diameter at soil surface, height and number of the all ES and TS seedlings were recorded. On the first day (7-7-2008) the ES for both species were also thinned if many of the seeds had sprouted.

Soil samples were taken to a depth of five centimeters using a 2.5cm diameter soil core sampler. Soil samples were collected twice: before the SRA treatment occurred and also afterwards. These were immediately placed in a cooler and later frozen to arrest the activity of soil bacteria, in order to preserve the available nitrogen levels at the time of collection. An AccuPAR[®] light meter was used to determine the levels of photosynthetically active radiation at soil surface (PAR_{ss}), which is characterized by having a wavelength of 400 -700 nanometers in width. Readings of PAR were obtained above the canopy as well as at the soil surface (PAR_{ss}) and were taken between the hours of 10:00 am and 2:00 pm, during periods of light to no cloud cover. PAR_{ss} measurements were taken on two different dates, at the time the seedlings and seeds were planted and four weeks later. Biomass samples were also collected twice, for the purpose of assessing the response of the plant community within the plot to SRA and GI. Biomass samples 30 cm in diameter were taken from randomly chosen plots, before and after nitrogen addition and grazing treatments. Samples were each placed into appropriately marked brown paper bags and left to dry completely for three to four months, at approximately 20 degrees Celsius, low humidity, and adequate air flow.

On the last day of the experiment (8-20-2008), when all of the ES and TS had begun to senesce they were harvested. This involved cutting the stems at the surface of the soil and placing them individually into appropriately marked brown paper bags. The samples were allowed to dry completely over a period of three months at approximately 20 degrees Celsius, low humidity, and adequate air flow. At the end of the three month drying period, the weight of the ES and TS specimens for both species was measured with a digital scale and recorded. The small seedlings were removed from the bag in order to find their weight. Larger specimens were placed in giant eagle brown paper bags and were weighed within the bag. The resulting weights of the larger specimens were later adjusted by subtracting the mean weight of ten giant eagle bags from them

Data Analysis

The biomass data was divided into four datasets and analyzed independently, split by seedling type and species; *A. theophrasti* emerged seedlings (ABES), *A. theophrasti* transplanted seedlings (ABTS), *A. hybridus* emerged seedlings (AHES), and *A. hybridus* transplanted seedlings (AHES). A Levene's test of homogeneity indicated high heterogeneity of variances, a characteristic of the data due to many small non-zero values. The heterogeneity was higher for the ES datasets than the TS due to high mortality, resulting in a high number of zeros (the few zeros existing in the TS datasets were removed from the analysis). A test of collinearity was applied before the quantile regression analysis could be completed, indicating through high variance inflation factor (VIF) values that collinearity existed between the independent variables. Due to the

importance of the interactions within the model, centering of the independent variables was necessary to improve the interpretability of the parameter estimates and produce more meaningful results (Schielzeth 2010). This was done by subtracting each level of the independent variables (GI, DPS, and SRA) by their means, resulting in new centered values for use in the analysis.

To test the whole plot affects of GI and SRA and the split plot affect of DPS on the success of the ES and TS seedlings, quantile regression analysis and the Tobit analysis were used. Quantile regression is not based on the assumption of a normal error distribution (Cade and Noon 2003) and is robust when applied to heterogeneous datasets, so transformation of non-normal data is not always necessary making it possible to analyze the TS datasets using the original dry weight data. It was necessary to transform both the ES datasets due to high heterogeneity of variances. The predicted values produced by the quantile regression procedure were used to create 3D surface plots of the predicted response for the chosen quantiles, using 95% confidence intervals. A 3D surface plot was also created from the predicted values produced by the Tobit analysis, for the AHES data set. The seedling numbers recorded on 7-7-2008 were also analyzed using the quantile regression procedure.

Only the second set of light readings collected on 7-26-2008 were relevant to the analysis, because they were taken after the application of SRA and GI to the plots. In order to analyze the PARss light readings, they were first converted to percentages of PARss by dividing the PAR readings taken at the soil surface by the PAR readings taken

above the canopy. These values were then analyzed using quantile regression of the median quantile, because several attempts at transformation were unsuccessful in correcting the high heterogeneity of variances within the dataset. Both means and predicted quantile surface plots were created to show PARss at varying treatment combinations. Species and seedling type were not included in the analysis of PARss.

The seedling count data was first transformed using a simple square root transformation. The transformed data was then analyzed using a two-way ANOVA, with the independent variables DPS and SRA. GI had not been applied at the time of data collection and so was excluded from the analysis. Seedling type was not considered in the analysis, but species was included as a variable to take into account seed size when predicting invader success.

Model Application

In order to compare the results of this study against a model constructed by Renne (2010), the means for all sixteen treatment combinations (ISP) were plotted against DPS and SRA. The data was further divided by GI in order to create eight separate datasets to be analyzed in SPSS 16.0. Eight, split plot two-way ANOVAs were run on each of the data sets respectively, using the whole plot affect of SRA and the split plot affect of DPS. The sixteen means calculated as part of the ANOVA outputs for each of the data sets was placed onto a worksheet in Sigma Plot 11.0, to create the eight three dimensional graphs (figures 2 and 3). Invader success probability (ISP) is represented by

the mean dry weight (g) of the harvested specimens across all 16 treatment combinations of SRA, DPS, and GI. The sixteen means were plotted against DPS and SRA, for comparison against a model created by Renne (2010). The Renne model was constructed from empirically derived data in order to predict invader success probability (ISP).

Results:

Dry Weight Analysis

Invasion success of our focal invaders depended strongly on shifts in local ecological conditions and importantly, when these changes corresponded with different life history stages. For established and emerging seedlings of both species, there was a qualitative differential response across most treatment combinations means (Figs. 2 and 3). In particular, ES ISP was generally positive non-zero values only in the largest DPSs whereas TS ISP increased similarly across DPS and SRA gradients for both species (figs 2a, 2b and 3a, 3b). Both Species of TS seedlings displayed a gradual increase in mass toward the intersection of $DPS = 4$, $SRA = 4$ (Figs. 2a, 2b and 3a, 3b).

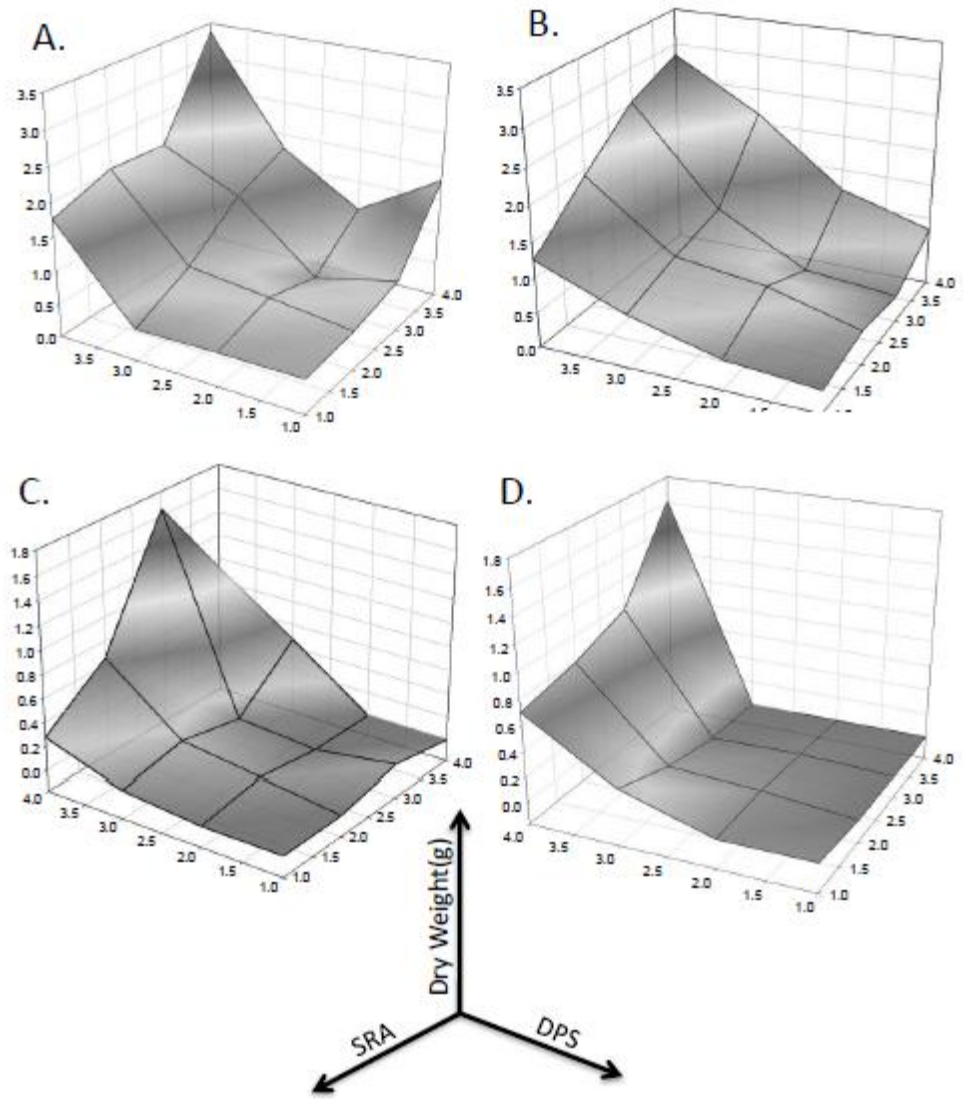


Figure 2. - $\ln(\text{dry weight}+1)$ transformed, dry weight (g) means for all treatment level combinations: A. Low GI, ABTS; B. High GI, ABTS; C. Low GI, ABES; D. High GI, ABES.

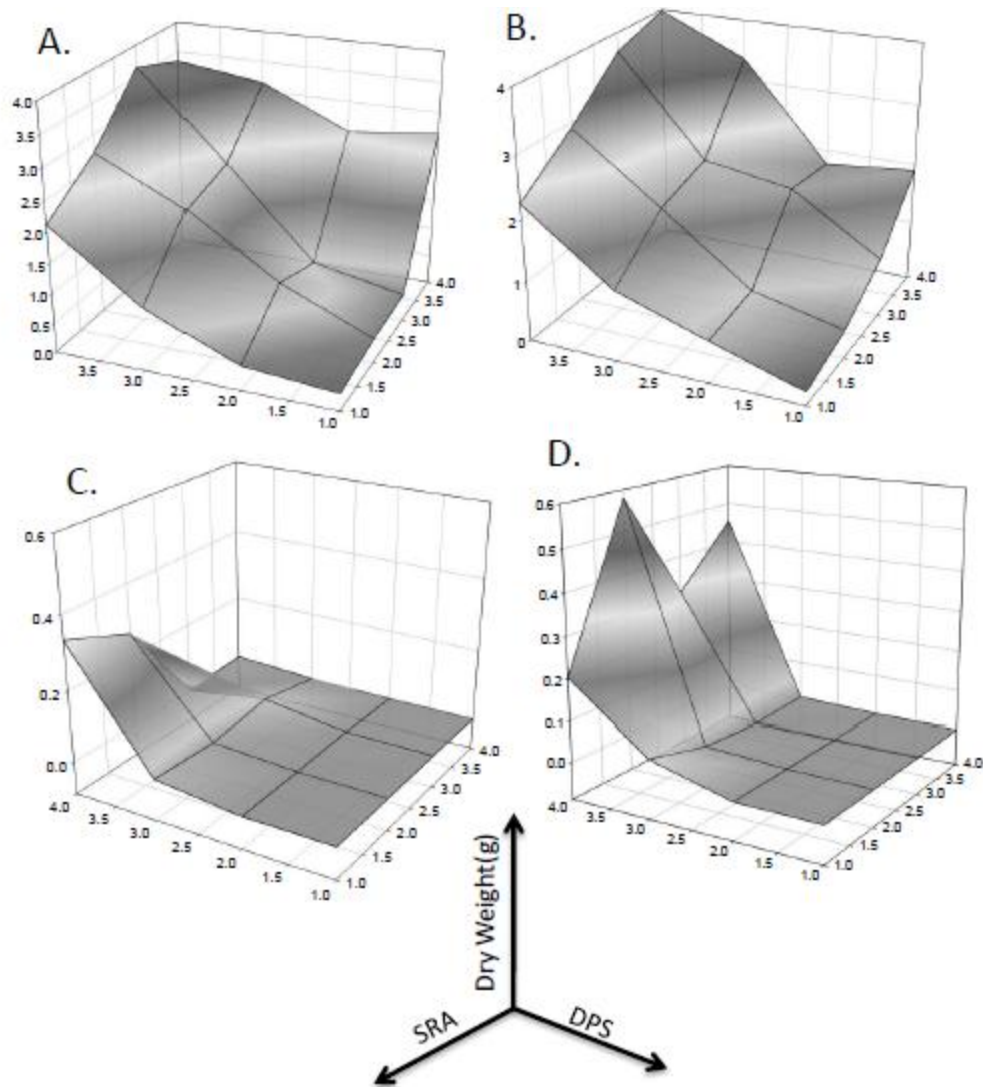


Figure 3. - $\ln(\text{dryweight}+1)$ transformed, dry weight (g) means for all treatment level combinations: A. Low GI, AHTS; B. High GI, AHTS; C. Low GI, AHES; D. High GI, AHES.

In contrast to the AHES response to the smaller disturbance patches, dry weight increased for the AHTS seedlings in the low GI plots for $\text{DPS} = 4$, $\text{SRA} = 1$. Figures 3d and 10b differed and this may be due to the heteroscedastic nature of the AHES dataset, resulting from a high frequency of zero's and low non-zero values. The lack of response

for the higher SRA levels along $DPS = 4$ for both figures 10a and 3c may be due to a lack of tolerance to the high dissolved urea levels by the young seedlings.

Unlike the ES who only had positive ISP in the largest DPS, TS dry weight increased within the small disturbance patches for both AHTS and ABTS with increasing SRA (figs 2 and 3). $DPS*SRA$ is significant for both AHTS and ABTS ($p < 0.0500$) (tables 1 and 2), indicating the interaction of DPS and SRA increased invader success for the TS seedlings in small sized disturbance patches

As predicted, increases in seedling mass were observed within small DPS for large SRA treatments because of grazing (Figs. 2b and 3d). However, GI only increased ISP for the AHES seedlings (Table 4, $GI p < 0.001$). The lack of response in the means graphs for the AHTS, ABES, and ABTS seedlings is consistent with the regression results, as GI is only significant for ABES in the 0.05 quantile and not at all for AHTS (tables 2 and 4). (NOTE: For all three quantile regression analyses the 0.05 quantile did not perform well due to the high number of zeros and small values contained within that quantile, which was expected.) The response for the ABTS was significant, but negative as the relationship between ISP and high GI for ABES and ABTS is reversed. The effects of SRA on ISP were greater ungrazed relative to grazed areas, particularly for AHES and ABTS. Seedling dry weight for AHES only contained non-zero values for the first treatment level of nitrogen in $DPS = 4$, which differs from AHES high grazing intensity (figs. 3c and 3d, fig 10.). The reduced response of the low GI seedlings is supported by a significant $GI*SRA$ interaction for AHES ($p < 0.05$, Table 4).

Figure 4. ABTS low GI. The predicted response for the 0.95 and 0.05 quantiles.

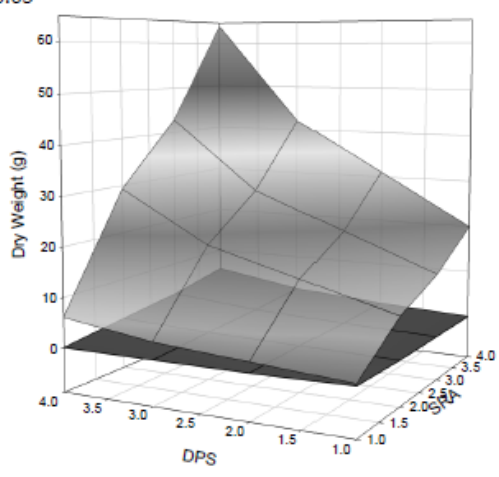


Figure 5. ABTS high GI. The predicted response for the 0.95 and 0.05 quantiles.

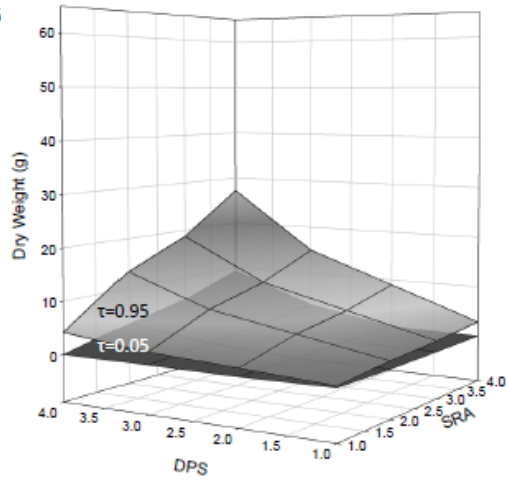


Table 1. ABTS quantile regression results. (P-values, * if $\alpha < 0.05$)

I.V.	$\tau = 0.05$	$\tau = 0.95$	DF
GI	0.5642	0.8177	1
DPS	<0.0001*	0.0028 *	3
SRA	0.0020*	<0.0001 *	3
GI*DPS	0.1288	0.0488 *	3
GI*SRA	0.8438	0.6397	3
SRA*DPS	0.0004*	0.0313 *	9
GI*DPS*SRA	0.3568	0.2036	9

As expected, invader life history stage itself greatly influenced the maximum ISP for both species. The responses between the respective ES and TS datasets are similar between treatment combinations for both the means and the predicted values, but the peak ISP achieved by the time of harvest differs depending on the size of the seedlings. The quantile regression analysis predicted an approximate 61% and 67% increase from the highest peaks of invader success for ABES to ABTS, for high and low grazing intensity respectively (figs. 4-7). The disparity between ES and TS was even higher for *Amaranthus* seedlings as there was nearly a 100% increase in the maximum ISP for both high and low grazing intensity *Amaranthus* seedlings (figs. 6, 7, and 10).

Figure 6 . AHTS low GI. The predicted response for the 0.95 and 0.05 quantiles.

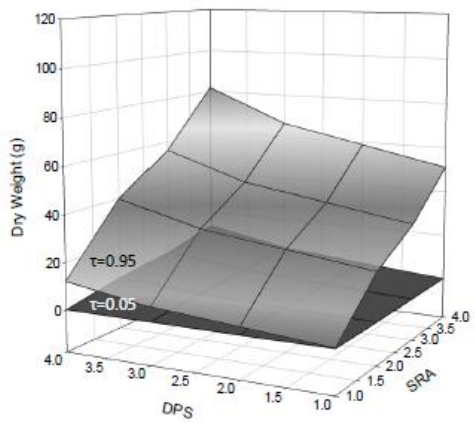


Figure 7. AHTS high GI. TI response for the 0.95 and 0.05 quantiles.

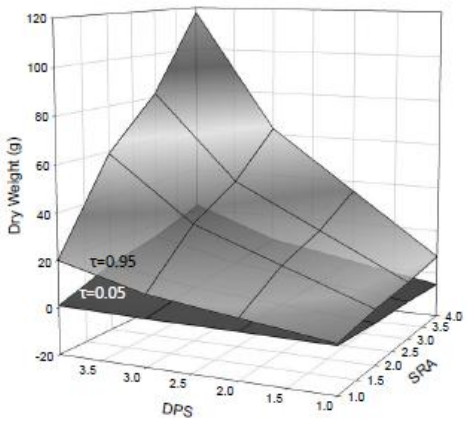


Table 2. AHTS quantile regression results. (P-values, * if $\alpha < 0.05$)

I.V.	$\tau = 0.05$	$\tau = 0.95$	DF
GI	0.8136	0.002 *	1
DPS	0.0014*	< 0.0001*	3
SRA	0.0510	< 0.0001 *	3
GI*DPS	0.1995	0.0327 *	3
GI*SRA	0.7652	0.0009 *	3
SRA*DPS	0.0137*	0.0002 *	9
GI*DPS*SRA	0.4518	0.0804	9

Figure 8. ABES low GI. The predicted response for the 0.95 and 0.05 quantiles.

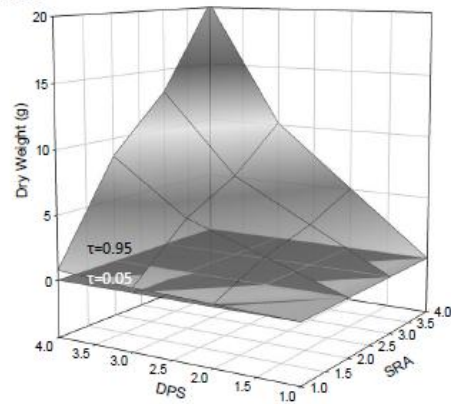


Figure 9. ABES High GI. The predicted response for the 0.95 and 0.05 quantiles.

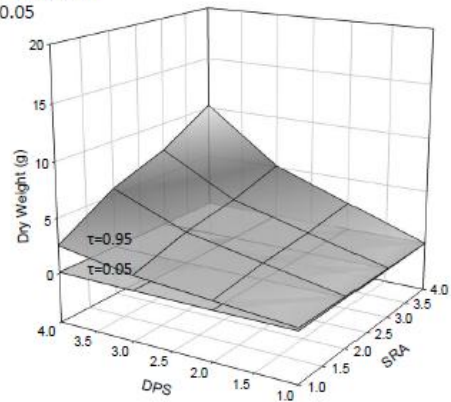


Table 3. ABES quantile regression results (Ln(y+1) transformed data). (P-values, * if $\alpha < 0.05$)

I.V.	$\tau = 0.05$	$\tau = 0.95$	DF
GI	< 0.0001*	<0.6526	1
DPS	< 0.0001*	< 0.0001*	3
SRA	< 0.0001*	< 0.0001*	3
GI*DPS	< 0.0001*	0.6814	3
GI*SRA	< 0.0001*	0.0136*	3
SRA*DPS	< 0.0001*	< 0.0001*	9
GI*DPS*SRA	< 0.0001*	0.0019*	9

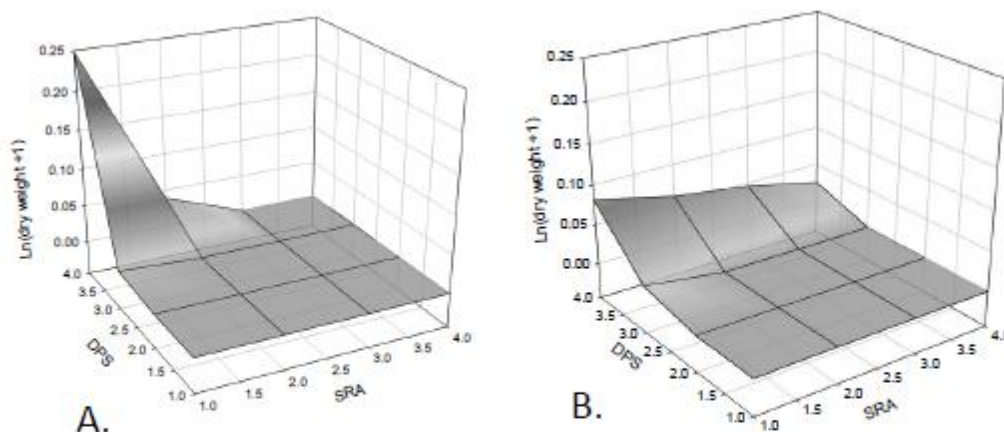


Figure 10. AHES Tobit Analysis predicted response; A. Low GI, B. High GI.

Table 4. AHES Tobit Analysis results. (* if $\alpha < 0.05$)

I.V.	P-values	DF
GI	0.0050 *	1
DPS	< 0.0001 *	3
SRA	0.0146 *	3
GI*DPS	0.0030 *	3
GI*SRA	0.0037 *	3
SRA*DPS	0.0475 *	9
GI*DPS*SRA	0.0078 *	9

Seedling and PARss Analysis

ES number was influenced differently by DPS and SRA for both species. As expected, DPS increased establishment for both species ($p < 0.000$) but SRA only increased the number of ABES. DPS was the only factor to affect AHES, as stated previously; we witnessed some seedling mortality, presumably because high levels of SRA were harmful to AHES seedlings.

Table 5. 2-way ANOVA results for square root transformed seedling number ABES data (P-values, * if $\alpha < 0.05$).

I.V.	df	F	P-values
DPS	3	74.8	0.000*
SRA	3	3.6	0.016*
DPS*SRA	9	1.7	0.086

Table 6. 2-way ANOVA results for square root transformed seedling number AHES data (P-values, * if $\alpha < 0.05$).

I.V.	df	F	P-values
DPS	3	8.9	0.000*
SRA	3	1.5	0.224
DPS*SRA	9	1.2	0.295

Quantile regression analysis of PARss indicated significant positive main effects for GI and DPS and negative effects for SRA ($p < 0.0004$), but no interactions were significant (table 7). However, there may be a potential interactive effect of GI*DPS ($p = 0.0605$), as there is a 30% increase in the PARss predicted response at the lowest disturbance patch and a 50% increase for the highest disturbance patch size at high grazing intensity (fig. 12).

Table 7. Quantile regression results for PARss (P-values, * if $\alpha < 0.05$).

I.V.	$\tau = 0.05$	df
GI	< 0.0001*	1
DPS	0.0003*	3
SRA	< 0.0001*	3
GI*DPS	0.0605	3
GI*SRA	0.7808	3
DPS*SRA	0.5869	9
GI*DPS*SRA	0.1426	9

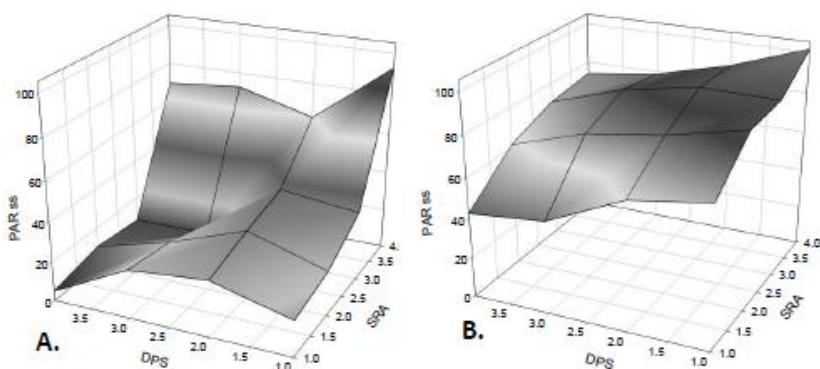


Figure 11.
A. Low GI PARss, B. High GI PARss

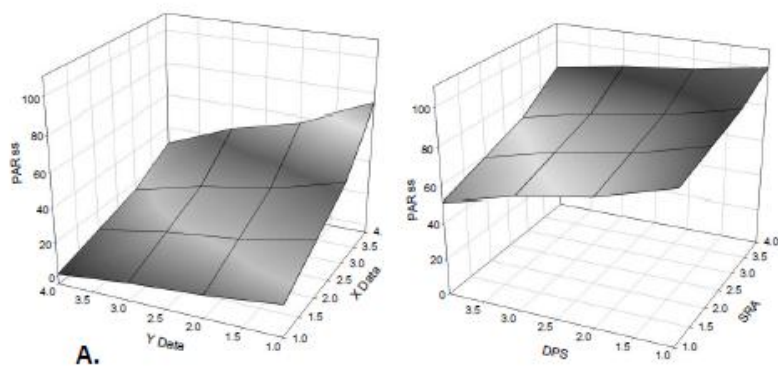


Figure 12.
Quantile regression results, $\tau = 0.50$
A. Low GI PARss, B. High GI PARss

Discussion

Effects of SRA and DPS on life history stage

Shifts in above- and below-ground resources are a major driver of spatiotemporal variability in community invasibility (Burke and Grime 1996; Proulx and Mazumder 1998; Davis 2000; Rajaniemi 2002; Huston 2004). However, the timing of shifts in resource availability is not only important to existing propagules but to invaders of later life history stages as well (Renne et al. 2006). The addition of nitrogen changes the availability of other resources, particularly light, because of increased productivity (Rajaniemi 2002). In our study, the effects of manipulating below- and above-ground resources with varying concentrations of dissolved urea were observed. Increased nitrogen generally improved the competitive ability of the transplanted seedlings for light overall, which enabled them to achieve a higher ISP across all disturbance patch levels (figs. 2 and 3). The relationship between higher TS invader success due to increased productivity is further supported by a significant $DPS \times SRA$ for both species (Tables 1 and 2).

This response was not seen in the ES datasets, as there was little to no increase in ISP within all but the largest DPS levels (figs. 2 and 3). Increased productivity from higher nitrogen availability may reduce light availability to such an extent that establishment from available propagules is nearly zero (Davis et al 2000, Foster 2001), particularly within smaller disturbance patches. However, larger soil disturbance patches can nearly eliminate competition for light, nutrients and water (Burke and Grime 1996;

Davis et al. 2000; Takehiro et al. 2009), which explains why the ES response was mostly limited to our largest disturbance patches (i.e., DPS = 4). A reversal in this trend was observed in the low grazing intensity AHES at the highest SRA level suggesting that the higher urea concentration may have increased seedling mortality for *A. hybridus* (L.) (figs. 3c, 10a; personal observation). This is further supported by the lack of significance of SRA for AHES, as SRA only had a positive effect on ABES and an observed negative effect on the AHES, particularly for the low grazing intensity seedlings (tables 5 and 6). Overall the maximum ISP for TS seedlings was greater than the ES seedlings by 65 and 100% for *A. theophrasti* (L.) and *A. hybridus* (L.) respectively. This finding suggests relaxation of available limiting resources (below ground in particular) TS ISP more than that of ESs. Analysis of seedling number for the ES datasets revealed differing effects of DPS and SRA on successful germination of each species (tables 5 and 6) and the increase in establishment due to DPS was expected and true for both species.

Invader size, DPS, SRA, and Grazing Intensity

Increasing productivity via nitrogen addition has been shown to decrease the success of lower growing, smaller plants within a community (Goldberg and Miller 1990; Bakker et al. 2006). In our study, increasing soil resources generally increased ISP for all TS seedlings. However, SRA had the opposite effect on ES and some of the TS seedlings, reducing invader success by increasing the biomass of the surrounding neighborhood and thus reducing light availability to the seedlings (Goldberg and Miller 1990). In the TS high grazing intensity treatments, the (potential) counteracting negative effects of SRA were reduced by removing the added biomass. I note the effects of

grazing intensity (GI) were not as pronounced as expected, most likely because I only implemented one extra “grazing” event and this likely did not represent a truly overgrazed pasture.

A closed canopy of well established native plants is a major factor in preventing successful invasion (Burke and Grime 1996; Bakker 2006; Foster 2001). Grazing by large herbivores can increase light availability while simultaneously increasing productivity through nutrient deposition, leading to enhanced germination and seedling establishment (Rajaniemi 2002; Bakker 2006). Increased PARss from our grazing treatment were significantly higher for the high GI plots (figs. 11, 12, table 7) and as expected, the high GI treatment increased ISP for AHES (figures 3d and 10b). Despite an SRA-induced productivity increase, the reduction in light competition within high GI plots increased ISP for the ES seedlings of AHES, particularly within the smaller DPS. There was not predicted increase in ISP due to grazing intensity for the other three datasets.

Overall, high GI increased the maximum ISP for *A. hybridus* (L.) (Fig.s 6 and 7). However, this response was reversed in *A. theophrasti* (L.) and may be because of fundamental differences in water use efficiency. *A. hybridus* (L.) is a C4 plant, which is not as water-limited as the C3 plant, *A. theophrasti* (L.) (Costea et al. 2004). High GI can decrease water availability through an accelerated uptake by the surrounding neighborhood and amplify the threat of desiccation to small, emerging seedlings contained within disturbance patches. Considering how these species differ, water stress

due to high GI is a reasonable explanation of the significant reduction (GI $p < 0.05$, tables 1 and 3) in ISP by nearly half for both the ES and TS of *A. theophrasti* (L.) between high and low grazing intensity (Figures 4, 5 & 8, 9).

Conclusions and Study applicability

Grazing can increase or decrease invader success, depending on life history stage, disturbance regimes, nitrogen availability and presumably species-specific resource requirements. Thus, grazing is likely to exhibit idiosyncratic effects on invasibility, as we observed (Proulx and Mazumder 1998). Moreover, depending on invader size (ES vs. TS), thresholds in invader success exist across DPS, the magnitude of which increases with higher nitrogen availability levels. This indicates that the timing of resource shifts can dictate invasion success, depending on when they coincide with particular life history stages.

This study may have high applicability by giving pasture managers some control over the extent the effect their livestock have on the disturbance regimes and community dynamics of the pasture ecosystem. During periods of high soil moisture cattle trampling has the potential to cause extensive damage to the below ground tissue of the existing forage species, resulting in large bare patches. As this research has shown, large bare patches coupled with grazing disturbance and the inevitable nutrient deposition by cattle, in the right combination can facilitate the dominance of a pasture ecosystem by unpalatable invaders. Knowledge of these factors can assist pasture managers in choosing the appropriate stocking and grazing rotation for their respective grasslands

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