Heterogeneous Stress Response in a Clonal Invader (Imperata cylindrica): Implications for Management

Sarah Grace Sanford
University of South Florida, sgrace.barry@gmail.com

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Heterogeneous Stress Response in a Clonal Invader (*Imperata cylindrica*): Implications for Management

by

Sarah Grace Sanford

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
Department of Integrative Biology
College of Arts & Sciences
University of South Florida

Major Professor: Gordon A. Fox, Ph.D.
Peter Stiling, Ph.D.
Earl McCoy, Ph.D.

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Dedication:

I dedicate this work to the memories of Maureen Dangleis and Lorriane Barry. Two such ladies there have never been, I don’t know who I’d be without them.

I’d like to thank Gordon Fox for his patience, support, and dedication, as well as my committee for their time. I’d also like to thank my undergraduate assistants Alli Kaplan and Ulviye Menekseoglu, without whom I’d still be counting, measuring, and weighing. A very special thank you goes out to Monica and Keith Downer for their unwavering facilitation and involvement, be it in the field, the lab, or the porch. Special kudos to my longest travelling assistant, Therese-Jo Dangleis, who flew over a thousand miles to spend two days in a 110° F greenhouse, just because she loves me that much. Thanks Mom! Much appreciation is also due my father, the very first to teach me the importance of observation, how to keep a log, and whom’s gardens made my first lab. In turn, thanks is due to my wonderful step mother Lori, for her constant reassurance and support. Thanks YESM!

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Abstract:

Life history traits such as growth, survival, and clonality can vary within a population. When such variation exists in a population of an invasive species, it can affect population dynamics, and if any part of the variation has a genetic basis the population can evolve in response to control regimes. Evolutionary responses to control efforts may shift the population towards a few more resilient genotypes, or towards different types in different microenvironments, depending on the scale of gene flow with respect to the patchiness of the environment. The purpose of this study is to examine whether the application of stress similar to control efforts (light level manipulation and biomass removal) results in varying emergence, growth, and survival rates between samples taken from spatially separated patches of the invasive clonal grass Imperata cylindrica. Accelerated Failure Time (AFT) and logistic regression models were fit to survival, emergence and growth data collected from two experiments in which samples collected from four spatially separated Imperata cylindrica patches were exposed to light level manipulation and biomass removal. Patch identity plays a large role in explaining variation in time-to-emergence, time-to-death, and probabilities of emergence and survival, especially under stressed conditions. Rhizome and above ground biomass characteristics also play substantial roles in explaining variation in emergence, survival, and growth, though more so under non-
stressed conditions. Our results warrant further study of heterogeneous responses to stressful conditions, especially those imposed under control and management regimes. This heterogeneity may have important impacts on population processes such as maintenance, expansion, and gene flow.
1.0 Introduction:

1.1 Demographic Heterogeneity:

Variation among individuals in survival and reproductive rates within a population, known as demographic heterogeneity, is common to all natural populations. This variation can be the result of a number of factors including an organism’s age, size, or stage in life. Other sources may include genetic variation, spatial heterogeneity, maternal effects, exposure to stress, or neighbor effects as in density dependent populations (Kendall et al. 2011). When modeling a population’s growth or viability, demographic heterogeneity is often confused with demographic stochasticity. Demographic stochasticity is the variation in demographic parameters (such as survival and reproductive rates) within a population that results from random occurrences. The difference between demographic stochasticity and heterogeneity is best illustrated with an example that utilizes the flip of a coin. Consider four coin flips. The expected result contains two heads, and two tails. Both stochasticity and heterogeneity cause unexpected results, one head and three tails for example. The difference between stochasticity and heterogeneity lies in why an unexpected result is obtained. In the stochastic scenario, the same coin is flipped four times, with an unexpected result due
solely to chance. The heterogenic scenario however uses four different coins with different weights, each flipped once.

Demographic heterogeneity has consequences in both the ‘immediate’ dynamics of a population, and in the longer term through impacts on natural selection. Variation in survival and reproductive rates can increase population growth rates, change stable age or stage distributions, and the rate at which these distributions are approached (otherwise known as the dampening ratio). This variation can also lead to adaptations including changes in life history, and to environmental variation including stress (Kendall & Fox 2002). As such, heterogeneity in demographic parameters such as survival, growth, and clonality can play a large role in determining a population’s success. Over the past 20 years it has been increasingly recognized that studies of variation may help predict the potential for populations of invasive species to grow as well as to evolve in response to management practices (Barrett 1992; Van Driesche & Bellows 1996; Sakai et al. 2001).

Evolutionary adaptation to control efforts resulting in varying phenotypes may take a number of different forms. For example, if there is little gene flow between populations or subpopulations, local adaptation to environmental conditions (including control efforts) may lead to selection for different genotypes in different locations (Proffitt et. al. 2003). If there is considerable gene flow and control efforts are consistently applied across different types of sites, adaptation can be to conditions experienced by “average individuals” in the population. Finally, populations may adapt to the unpredictability of the environment, as when control efforts are applied
inconsistently. Whether natural selection moves a population towards a few more resilient phenotypes, or towards different types in different microenvironments, depends on the scale of gene flow with respect to the patchiness of the environment. Phenotypic plasticity may play an important role in permitting invasions because colonists must be able to cope with a range of environmental conditions (Baker 1965, 1974; Gray 1986). Additionally, phenotypic plasticity in response to stress may ultimately permit invasive populations to escape control efforts.

Demographic heterogeneity within populations of clonal plants may occur at the levels of ramets, genets, or both. While ramets represent potentially independent units of a clone, genets represent unique genetic individuals which may be composed of multiple ramets. Since ramets are genetically identical (ignoring the case of somatic mutation), the distribution of traits in the population changes with (1) the number of distinct clones or genets, (2) the relative growth rates of the different genets under the prevailing suite of microenvironmental conditions at the site, (3) the rate of viable seed production, particularly seeds produced through outcrossing, (4) the survival and growth of resulting seedlings relative to environmental conditions (Proffitt et al. 2003) and (5) the amount of phenotypic plasticity among ramets and genets that result in varying survival, growth and reproductive rates.

Clonal growth typically leads to clusters of ramets, resulting in a spatial genetic structure in which there is high genetic similarity at short distances while genetic distances between ramets located further apart are
expected to be larger, likely because they are thought to originate from different genets (Capo-chichi et al. 2005). Spatial genetic structure also is a consequence of limited dispersal of both seeds and pollen (Epperson 2003). Spatially distinct, monospecific stands referred to as ‘patches’ are often thought to be clusters of genetically identical or closely related, ramets. However, even in populations of clonal grasses there can be significant genetic variation on at small spatial scales. A recent study of non-native Phragmites australis revealed that 96% of patches (defined as robust, isolated stands located at least 10 meters apart) examined in one location were composed of multiple genotypes. Plants in patches that were physically closer together were genetically more similar than those farther apart (McCormick et al. 2009). Similarly, work examining genetic structure in a population of the clonal grass Setaria incrassata found that the average genetic difference was greater between patches (defined as spatially discrete, monospecific stands) than within patches among 55 distinguishable genotypes from 3 patches (Bryson & Carter 1993).

Genotypic variation between clonal plants populations is also common. A literature survey reviewing patterns of genotypic diversity in clonal plant species by Ellstrand and Roose (1987) found genetic variation within geographically isolated populations of all 5 species in Poaceae reviewed (Argostis stolonifera, Festuca rubra, Holcus mollis, Puccinellia x phyrganodes, and Spartina patens). Genetic diversity at the population level can become a source for further diversification at the local level when control efforts provide a mechanism for gene flow among populations.
Genetic variation in combination with and resultant from a history of multiple introductions has been shown to facilitate invasion success. Recent studies by Lavergne & Molofsky (2007) examining genetic variation both among and within native (European) and invasive (North American) populations of the perennial wetland grass *Phalaris arundinacea*, revealed that the invasive genotype associated with North American populations evolved after multiple introductions of genetic material native to different European regions. The resulting genetic diversity and increased evolutionary potential in North American populations allowed for rapid selection of novel genotypes with greater vegetative colonization abilities and phenotypic plasticity. Invasive genotypes of *P. arundinacea* emerge faster and exhibit higher tillering and leaf production rates, indicating greater potential for clonal spread and leaf canopy expansion. Similarly, invasive genotypes produce significantly more above-ground biomass than native genotypes. These enhanced capabilities of invasive genotypes explain the greater aggression of populations found in North America in comparison to native European populations. Additionally, invasive populations exhibited larger broad sense heritability for traits including relative growth rate, tillering rate, below ground biomass and emergence time, resulting in increased potential for response to natural selection towards aggressive genotypes. Further experiments by the authors indicate that phenotypic plasticity may enhance invasion success in introduced populations of *P. arundinacea* (Lavergne & Molofsky 2007).
The purpose of this study is to examine whether the application of stressful conditions similar to those experienced under control efforts results in varying emergence, growth, and survival rates in the invasive clonal grass *Imperata cylindrica*. If there is phenotypic variation, selection of traits increasing the resistance of *I. cylindrica* to control efforts is likely, further complicating already ineffective control efforts. The stresses employed in this study include light level manipulation and the removal of biomass to mimic conditions experienced under mechanical control efforts, namely shading, discing, and mowing. Our intent is not to test the hypothesis that light level is a strong predictor of emergence, survival and growth, but rather to ask if variation in response to stress exists, and if so, how much. To test our hypotheses, two experiments were performed. The first experiment examines how patch identity and below ground biomass (rhizome mass and length) affect emergence and survival in light-stressed and unstressed conditions. The second experiment examines how patch identity and above ground biomass (stem abundance) affect survival and growth under grazed, light-stressed and unstressed conditions.

1.2 Species:

Cogongrass (*Imperata cylindrica*) is a warm-season, rhizomatous perennial grass, native to South East Asia that can be found throughout the tropical and subtropical regions of the world, thriving in areas of natural and particularly human disturbance. It was at one time reported to be established on over 500 million hectares worldwide (Holm et al. 1977; Dozier et al.
1998). Once noted as the seventh most troublesome weed worldwide (Holm et al. 1977), cogongrass generally invades areas after a disturbance, such as natural fire or flood, mining/land reclamation, forest operations, or highway construction and maintenance. Once established, cogongrass out-competes native vegetation, forming large solid stands with extremely low species diversity and richness (MacDonald 2004). In its native range cogongrass is a pyrogenic species, relying on fire for survivability and spread (Holm et al. 1977), while invaded areas near human developments tend to be fire suppressed. Cogongrass fires can be very intense, limiting natural secondary succession (MacDonald 2004; Eussen & Wirjahardja 1973; Seavoy 1975; Eussen 1981; Lippencott 2000). As such, successful invasion by cogongrass can alter normal fire cycles of communities resulting in shifts in assembly from more diverse ecosystems to species-poor grasslands (Lippencott 2000).

Cogongrass is currently listed as a noxious weed by both the Florida Department of Agriculture and Consumer Services and the United States Department of Agriculture. In Florida, cogongrass is widespread, occurring throughout the state. Here, cogongrass typically persists on disturbed lands including reclaimed phosphate mines as well as roadside ditches. A survey of Florida highway rights-of-way conducted during 1984-85 to determine the occurrence and severity of cogongrass infestation found widespread distribution of cogongrass from the north-central region southward through the central Florida ridge north of Lake Okeechobee, with the highest frequencies in counties where cogongrass was used for forage and soil stabilization during the 1950s. These infestations probably were established
during extensive roadway construction and routine maintenance which used rhizome-contaminated fill soil. (Willard et al. 1990) This wide distribution along transportation systems maintained by the Florida Department of Transportation may provide a ‘gene-flow highway’ as current control practices include mowing, during which living plant material may be transported long distances.

1.2.1 Physiology:

Cogongrass is a C₄ species best adapted to full sun, yet it also thrives in moderately shaded conditions due to a light adaptation involving changes in specific leaf area and leaf area ratio (Paul & Elmore 1984). This allows tolerance of up to a 50% reduction in sunlight (Patterson 1980). Additionally, a light compensation point of 32 – 35 $\mu$ mol m$^{-2}$ s$^{-1}$ indicates an ability to survive as an understory species (Gaffney 1996; Ramsey et al. 2003). Unlike other rhizomatous grass species, light has a positive effect on cogongrass sprouting, evidenced by a Holm study (1977), which reports an increase in sprouting of 2-3 times in light when compared to dark.

Cogongrass rhizomes can comprise over 60% of total plant biomass, and it is this low shoot to rhizome ratio that is attributed to rapid re-growth after burning or cutting (Sajise 1976), as fragments weighing as little as 0.1 g successfully form new plants (Ayeni & Duke 1985). In addition to rhizome production, cogongrass invades and persists through: 1) adaptation to poor soils and drought, 2) prolific wind disseminated seed, and 3) the ability to
withstand and thrive in a fire-based ecosystem (Hubbard et al. 1944; Holm et al. 1977; Brook 1989; Dozier et al. 1998; MacDonald 2004).

To date, research on the relationship between apical dominance and shoot re-growth from rhizomes has provided conflicting results. A lack of axillary bud development due to a lack of shoot emergence from rhizome sections with the apex removed was reported by Wilcut et al. (1988). However, subsequent work conducted by Gaffney (1996) reported shoot development confined to the apical region when the apex was intact, while removal of the apex promoted random shoot development along the length of the rhizome. Manipulative experiments utilizing plant growth regulating hormones including indole-3-acetic acid (IAA) conducted by Shilling & Gaffney (1997) and English (1998) support the role of apical dominance in cogongrass.

Recent work examining genetic variation in populations near the epicenter of introduction into the southeastern U.S. reveals three major genetic subgroups among nine sites tested, with no relationship between gene flow and geographic distance as well as genetic and geographic distances, suggesting that the invasion dynamics of cogongrass into the southern U.S. is primarily through anthropogenic activities and to the lesser extent through natural forces. (Ludovic et al. 2008) Genetic variation and distribution among cogongrass populations throughout the rest of the southern U.S. has yet to be analyzed. The sale of ornamental cogongrass varieties under the names Rubra, Red Baron and Japanese Blood Grass (var. Rubra, or var. koenigii) present concern over the potential for hybridization
between ornamental ecotypes and weedy biotypes found in the southern U.S. (MacDonald 2007). These ornamental varieties are known to survive far north of weedy biotype range limits, and as such stand to extend range limits of both biotypes if hybridization occurs (MacDonald 2007). Studies suggesting a high degree of variability and potential hybridization within the species further elevate the importance of this issue (Gabel 1982; Hall 1998; MacDonald 2007).

1.2.2 Control:

Many studies have evaluated the efficacy of single and combined herbicidal and mechanical treatments on single or few large colonies of cogongrass in terms of above ground and rhizomatous biomass. As long-term control of cogongrass is thought to be largely dependent on rhizome elimination, basing perennial weed control evaluations on foliar responses alone may cause overestimation of long term treatment efficacy (Willard et al. 1996). To date, no study performed has revealed a control regime providing complete elimination. At best, these studies have found a few ‘acceptable’ (> 80% reduction in rhizome biomass) control methods, most of which include multiple combined treatments of glyphosate, or imazapyr, with disking both before and after herbicide application. (Willard et al. 1996) One recent study found that herbicidal treatments temporarily control above ground biomass with negligible effects on rhizome biomass while disking had no effect on foliar re-growth but did decrease rhizome re-growth. Even with
these treatments combined, full recovery of the colony was achieved by 24 months after control efforts ceased. (Ramsey et al. 2003)

There is some evidence that shade is useful in controlling cogongrass, perhaps because it induces changes in biomass dry weight, partitioning and plant morphology (MacDicken et al. 1997). One study found a 26% reduction in rhizome biomass associated with a 50% reduction in light intensity (Ramsey et al. 2003), while another found that the relative growth rates (RGR) of *Imperata* shoots and rhizomes were reduced when subjected to a by 50% to 80% reduction in light intensity over a period of two to six months (Eussen 1977). Other work examining the effect of shade and glyphosate efficacy found that mean shoot number, dry weight and total rhizome production significantly decreased with increased shade in herbicide-free treatments. Additionally, increased shade severely depressed total nonstructural carbohydrate content in herbicide-free treatments, compared with less severe reductions in the herbicidal treatments. The authors suppose this carbohydrate depletion indicates that the increase in photosynthetic tissue from an observed increased shoot to rhizome ratio does not compensate for the reduction in light. (Moosavi-Nia & Dore 1979).
2.0 Methods:

2.1 Study Site:

Reclaimed phosphate mines have highly modified soils which are thought to hinder the establishment of native species in favor of non-native species that specialize in disturbed habitats (Tamang 2005). One such soil modification is the formation of clay settling areas (CSAs) characterized by high bulk density, poor drainage, high levels of P, K, and micronutrients, and pH of 7.0–8.3. These CSAs represent approximately 40% of the 85,000 ha of reclaimed phosphate mine lands in Florida, and are commonly dominated by Cogongrass (Langholtz et al. 2007; Van Loan et al. 2002).

Our study site encompasses 1 sq. mile of reclaimed phosphate mine known as Old Hopewell, located on Section 29, Township 29S, Range 22E, of Hillsborough County, Florida, at which cattle ranching is the predominant land use (Figure 1a). Hardwood oak communities (Quercus sp, Carya glabra, Liquidambar styraciflua, Acer saccharum ssp. floridanum, Quercus virginiana, Fraxinus americana) dominate uplands created by spoil piles and CSAs during active mining, while the majority of the property is dominated by seasonally grazed grasslands (Rhynchelytrum repens, Paspalum notatum, Bidens alba, Lantana camara, Phytolacca americana, Solanum capsicoides, Solanum viarum) and some swampy lowlands (Taxodium sp., Typha
domingensis, Eichhornia crassipes). All sample sites were located on open, unshaded grassland portions of the property.

2.2 Experimental Design:

Both experiments utilized an orthogonal factorial design. Factors considered in the below ground biomass experiment include patch identity and rhizome characteristics (length and mass), with two levels of light level manipulation as treatment. Samples were organized into a total of six blocks, three for each light treatment. Each block contained ten samples from each patch identity (A, B, and C) for a total of thirty samples, such that $N_{total} = 180$, $N_{light} = 90$, $N_{shade} = 90$, $n_a = 60$, $n_b = 60$, $n_c = 60$.

The above ground biomass experiment differs from the below ground biomass experiment in that factors considered include patch identity and above ground biomass (defined as the log-transformed stem count at the start of treatment) and contains an additional grazing treatment for a total of two treatments at two levels each, resulting in four combinations of treatments (shaded + un-grazed, shaded + grazed, light + grazed, light + un-grazed). Equal ratios of each size (small, medium, and large), patch identity (A, B, C, and D), and graze treatment (grazed and un-grazed) were divided into a total of six blocks, three for each light treatment. Each block contained ten samples from each of patches A and B, and five from patch D, for a total of thirty five samples per block such that $N_{total} = 210$, $N_{light} = 105$, $N_{shade} = 105$, $n_a = 60$, $n_b = 60$, $n_c = 60$, $n_d = 30$, $n_{grazed} = 105$, $n_{un-grazed} = 105$. 
2.3 Sample Collection & Processing:

In April of 2009, and November of 2010, rhizome pieces with attached stems and blades were harvested from distantly separated patches of *I. cylindrica* using hand trowels. Samples collected in April 2009 were used in the below ground biomass experiment, while samples collected in November 2010 were used in the above ground biomass experiment. Sample collection and processing methods were consistent between experiments. Patch selection criteria included ease of access, full sun exposure, significant (＞150 meters) separation from other selected patches, a minimum patch size of 3 meters\(^2\), and a healthy stem density such that interior die off wasn’t apparent (Figures 1b & 1c). Samples were taken haphazardly within the interior of the patch, from neither the advancing edge, nor the very center. During collection, samples were stored in 5 gallon plastic buckets containing moist soil to protect from sun and heat.

Immediately following collection, samples were potted in 6” square black plastic pots, using a 1:2 mix of coarse perlite to sandy potting mix (produced on site from local compost and soil), and grouped by patch identity. Samples were then allowed an average recovery period of 11 weeks during which they were watered regularly by hand. After the recovery period, surviving individuals from each patch identity were selected at random for experimental treatment.

For the below ground biomass experiment, before treatment began the above ground biomass was removed from each sample, and the pre-treatment rhizome mass (g) and length (cm) was recorded. Rhizome pieces
were then re-potted and tagged with patch and sample identification numbers before being divided into one of two light treatments, shade (S) and light (L). Samples subjected to light treatments were exposed to natural light conditions. Samples subjected to shaded treatments were placed in temporary outdoor shade cages constructed with two layers of 40% shade cloth. All samples were subjected to light manipulation for 9 weeks, starting July 15, 2009. Daily light exposure as measured from sunrise to sunset ranged from 14 hours and 49 minutes at the start of the experiment, to 12 hours and 5 minutes at the conclusion of treatment. All samples were watered by hand every third day for the entire nine week period. Emergence and survival data for each pot was recorded weekly.

For the above ground biomass experiment, before treatment began, the size category of each sample was determined using the log transformed number of stems (small $0 \leq 0.69$, medium $0.7 \leq 1.79$, or large $1.8 \leq$). Size category delineation was based on natural breaks in the log transformed number of stems. Subsequently, equal ratios of each size and patch identity were divided into one of four orthogonal treatment combinations of light, shade, grazed and un-grazed conditions. Samples were segregated by light treatment, while grazed and un-grazed samples were kept together. Light supplementation was provided for 12 hours daily by a 2 x 2 meter$^2$ light grid containing 16 evenly spaced lamps with EcoSmart 14 watt Daylight CFL© light bulbs. Samples subjected to shaded treatments were placed in a temporary shade cage, placed adjacent to the light grid. Daily light exposure was limited to 12 hours for the duration of the experiment. Stems in grazed
pots were trimmed to 10 cm above the soil line at the commencement of light treatment and measured weekly. Samples were subjected to treatment for five weeks, starting February 12, 2010. All samples were watered by hand every fourth day for the entire five week period. At the conclusion of the five weeks, the number of stems, blades, and the longest blade length of each pot was recorded. Survival data for each pot was recorded weekly.

2.4 Statistical Analysis:

All statistical analysis was performed using the statistical package R 2.12.1. To analyze factors concerning emergence and survival, data was pooled due to the low number of surviving samples. Both data on time to emergence and survival were analyzed with accelerated failure time (AFT) models (Fang et al. 2006; Fox 2001; Kalbfleisch & Prentice 2002). These models can accommodate censored data, in which the exact timing of the event is unknown. There are two kinds of censorship in these data. Plants still living at the end of the census were considered right-censored as of the last census. All other plants were considered to be interval-censored, meaning the true date of the event was between the census at which it was recorded and the prior census. AFT models can use a variety of error distributions and are therefore a standard approach for event-time data, which characteristically do not have symmetric errors. Models using logistic, loglogistic, lognormal, Gaussian, and Weibull distributions, as well as the exponential (constant mortality) distribution were fit to the data, after which
Akaike Information Criterion (AIC) values were used to choose among the models.

Secondarily, the cumulative probabilities of emergence, survival, and growth were modeled using logistic regression with binomial distributions. The use of these two different model types provides distinctive views on how predictors may affect the occurrence of an event. While AFT models use time to an event as a dependent variable, logistic regression uses the probability of an event’s occurrence as the dependent variable. This distinction is quite useful when trying to discriminate if a predictor changes the likelihood of an event, or its timing. For example, if investigating the proper dose of an herbicide or pesticide, logistic regression with a binomial distribution will provide the simple probability of death occurring after exposure to a specific dose, while an AFT model can describe how the time until death after exposure may change depending on dosage. In this study, logistic regression provides the cumulative probability of emergence, survival, or growth depending on predictors such as patch identity, rhizome mass and length, above ground biomass (defined as the log transformation of stem count) and the presence of grazing. Accelerated Failure Time (AFT) models illustrate how the time to emergence or death is affected by these same predictors. Both model types were subjected to a stepwise Akaike Information Criterion (AIC) procedure, which sequentially removed and added terms to the models to find the set of predictors that yielded the lowest AIC, otherwise referred to here as the ‘best-supported model’.
Decomposition of the sources of variation in both full and best supported models was performed by analysis of deviance. Analysis of deviance (type II) is a generalization of analysis of variance (Fang et al. 2006; McCullagh & Nelder 1989), used for cases such as with survival data and in logistic regression in which the residuals are not normally distributed. Type-II tests test hypotheses that are reasonably construed as tests of main effects and interactions in unbalanced designs, and are calculated according to the principle of marginality, testing each term after all others, except ignoring the term’s higher-order relatives. For example, in a three-way ANOVA with factors A, B, and C, the Type-II test for the AB interaction assumes that the ABC interaction is absent, and the test for the A main effect assumes that the ABC, AB, and AC interaction are absent but not necessarily the BC interaction, since the A main effect is not marginal to this term (Fox 1997). When residuals are not normally distributed, sums of squares (as used in ANOVA) are no longer useful to measure the discrepancy between model and data. Instead, the appropriate measurement is the model’s deviance, defined as twice its log-likelihood (Fang et al. 2006; Edwards 1992).

In addition to the use of two different model types, data sets from both experiments were analyzed in two different ways whenever possible. First, the full data sets for each experiment representing combined light treatments were modeled such that emergence, survival, or growth is predicted by the full set of predictors including light level and all possible interactions. Second, each data set for each experiment was subdivided into
light treatment and analyzed separately. Here, emergence, survival, or growth in each light treatment is predicted by the full set of predictors and all possible interactions. In the below ground biomass experiment, the full set of predictors used was source type (patch identity), rhizome mass, rhizome length, and light treatment, and the interactions between terms. In the below ground biomass experiment, the full set of predictors used included source type (patch identity), size, and light treatment the interactions between these terms, and grazing as an additive term only. In the case of growth, the subdivided data sets could not be analyzed, due to complete separation between predictor variables and outcomes.
Figure 1a. Old Hopewell Mine Reclamation Site. Total area = 1 sq. mi. Sample collection patches A (N 27° 55.773’ W 082° 08.488’), B (N 27° 56.003’ W 082° 08.617’), C (N 27° 56.003’ W 082° 08.617’) and D (N 27° 55.903 W 082° 08.512’).

Figure 1b. Old Hopewell Mine Reclamation Site Patch C.
Figure 1c. Old Hopewell Mine Reclamation Site Patch B.
3.0 Results:

3.1 Testing Emergence:

Emergence is tested in the below ground biomass experiment only. Figure 2 illustrates rhizome characteristics of both emergent and non-emergent samples in both light and shade treatments. While significant numbers of samples in both light treatments failed to emerge, more samples emerged under lit rather than shaded treatments. To analyze how rhizome characteristics, patch identity, and light level affect time-to-emergence, data representing emergent samples ($N_{\text{emerged}} = 72; n_A = 42, n_B = 17, n_C = 13$) was fit to a suite of AFT models with consideration of patch identity, rhizome characteristics, and light treatment as factors. Akaike information criterion (AIC) values indicate the loglogistic model as the best fit (AIC=154.611). Stepwise AIC evaluation retains all predictors and their interactions (the full loglogistic model) as the best supported model. Analysis of deviance reveals significant interaction effects between rhizome mass and light treatment ($p = 0.012$), rhizome mass, patch identity and light treatment ($p = 0.048$) and the highest order interaction between all predictors ($p >> 0.0001$). Following the full interaction term, the only independent predictor to be found significant was light treatment ($p > 0.0001$) (Table 1).
By fitting a logistic regression model with a binomial distribution to data from each light treatment independently, \((N_{\text{Light}} = 90, N_{\text{Shade}} = 90)\), most of the higher order interactions are decomposed. Here, the emergence probability for a sample (over the entire experiment) is predicted by patch identity, rhizome characteristics, and all possible interactions between terms. For light treatments, stepwise AIC evaluation retains only rhizome length and patch identity as relevant predictors. Analysis of deviance indicates that rhizome length \((p < 0.0001)\), in addition to patch identity \((p = 0.041)\) accounts for the most deviation explained by the model in light treatments (Table 2). For shaded treatments, the same analysis retains both rhizome mass and length as useful predictors of emergence probability, in addition to patch identity. Here, analysis of deviance indicates patch identity \((p = 0.0003)\) explains the most amount of deviance explained by the model, followed rhizome mass \((p=0.007)\), as well as the interaction between them \((p = 0.094)\) (Table 2).

Emergence curves generated by the accelerated failure time (AFT) model considering patch identity and light treatment provide a complex view of emergence behavior over time. Emergence probability varies widely by patch identity in light treatments, while occurring only in the first two weeks in shade treatments. Samples in light treatments from patch C continue to emerge until week 4, while samples from patch B emerge through week 7, and samples from patch A emerge throughout the entire experiment (Figure 3).
3.2 Testing Survival:

3.2.1 Below Ground Biomass experiment:

To examine how rhizome characteristics and patch identity affect time until death, survival data representing emergent samples \( N_{\text{emerged}} = 72; \ n_A = 42, \ n_B = 17, \ n_C = 13 \) from combined light treatments was fit to a suite of AFT models with consideration of patch identity, rhizome characteristics, and light treatment as factors. Akaike information criterion (AIC) values indicate the Weibull model as the best fit (AIC=210.88). Stepwise AIC evaluation retains all predictors, some second, and some third order interactions as relevant (Table 3a). Analysis of deviance of the best supported model reveals patch identity \( (p = 0.002) \) to be the strongest predictor effecting time-to-death, other than light treatment \( (p << 0.0001) \). Additionally, two second and third order interactions are important with respect to best supported time-to-death model. Both second order interactions include light treatment, and vary between patch identity \( (p = 0.016) \) and rhizome mass \( (p= 0.084) \) for the second term. Both third order interactions include rhizome mass and length, and vary between patch identity and light treatment for the third term \( (p < 0.001) \) (Table 3a).

Again, some of these higher order interactions can be decomposed by segregating the data by light treatment and modifying the model such that the light term is removed. In light treatments, rhizome mass \( (p= 0.006) \) is partly disentangled, and revealed to be the only significant main predictor in the full time-to-death model (Table 3b). In shaded treatments, both patch
identity and rhizome length are removed from a third order interaction with rhizome mass, but remain a part of a relevant second order interaction \((p = 0.063)\), in addition to being relevant main predictors \((p = 0.011, p = 0.027)\) (Table 3b). Logistic regression of the data such that cumulative survival probability is predicted by rhizome characteristics, patch identity and all possible interactions supports the conclusion that rhizome mass \((p = 0.016)\) is significant in explaining model deviation in light treatments, while patch identity \((p = 0.033)\) does so in shaded treatments (Table 4). This method does nothing however, to help clarify the higher order interactions between rhizome length, mass and patch identity in shade \((p = 0.093)\) or in light treatments \((p = 0.0005)\) (Table 4).

Survival curves generated by the AFT model (Figure 4) illustrate that survival chances of all patch identities remain relatively high in lighted treatments, while varying greatly between patch identities in shade treatments. Samples from patch A maintain the highest survival probabilities in both light \((\text{prob(survival)} = 0.91)\) and shaded treatments \((\text{prob(survival)} = 0.45)\) for the duration of the experiment. Samples from patches B & C show similar survival probabilities in light treatments, \((\text{prob(survival)} = 0.63, \text{prob(survival)} = 0.71)\), while demonstrating varying responses in shaded treatments \((\text{prob(survival)} = 0, \text{prob(survival)} = 0.3)\).
3.2.2 Above Ground Biomass experiment:

Similar to the below ground biomass experiment, survival data collected in this experiment was analyzed utilizing both AFT and logistic regression models. Results of AFT models are summarized in Table 5a and Table 5b, while results of logistic models are summarized in Table 6a and Table 6b.

To examine how patch identity, above ground biomass (stem abundance), grazing, and light level affect time-to-death, survival data (N=262; n_A = 68, n_B = 69, n_C = 95, n_D = 30) of combined light treatments was fit to the a suite of AFT models. The Weibull model was deemed best fit with the lowest AIC (511.615). Stepwise AIC analysis retains all main predictors in addition to several second order interactions as relevant to the best supported model (Table 5a). Analysis of deviance reveals light treatment (p >> 0.0001), followed by above ground biomass (p < 0.0001) to be important main predictors explaining time-to-death model deviance. In this instance, patch identity emerges as important as part of a second order interaction term with light treatment ((p = 0.0001) (Table 5a). Fitting the same data to a logistic regression model with a binomial distribution such that cumulative survival probability is now predicted by above ground biomass (stem count), patch identity, light treatment and their interactions, with grazing included as an additive term, reveals similar results but drops all second order interactions. In this analysis, above ground biomass (p < 0.0001), and patch identity (p = 0.034) explain the most model deviance, other than light treatment (Table 6a).
Segregation of the data into light treatments under the AFT model reveals differences in factors affecting time to death between light and shaded treatments. In shaded treatments, above ground biomass ($p > 0.0001$), patch identity, ($p > 0.0001$), grazing ($p = 0.741$) and the interaction between above ground biomass and grazing are retained in the best supported model of cumulative survival probability, while models of light treatments retain only patch identity ($p = 0.004$) and grazing ($p = 0.089$) as relevant terms (Table 5b) in explaining model deviance.

Re-examination of the logistic survival model with data segregated by light treatment eliminates the second order interaction between patch identity and light treatment, found in both logistic regression and AFT models utilizing combined light treatment data sets. In light treatments, patch identity ($p = 0.005$) explains the most model deviance, followed by above ground biomass ($p = 0.046$), however the reverse is true in shaded treatments. Here, above ground biomass ($p < 0.0001$) explains the most model deviance, followed by patch identity ($p = 0.003$) (Table 6b).

Survival curves in Figure 5 show survival of samples from all patch identities remain relatively high in light conditions, while varying greatly in shaded treatments. No deaths occur in samples from patches B, C or D in light treatments ($\text{prob(survival)} = 1$), though some samples from patch A did perish ($\text{prob(survival)} = 0.839$). Performance in shaded conditions varies among patch identities, similar to results found in the below ground biomass experiment. Samples from patch A fair the best in shade ($\text{prob(survival)} = 0.471$) compared with samples from patches B and C ($\text{prob(survival)} = 0.18$ -
0.31). In this case, samples from patch D have the worst survival probability, with no chance of survival by the fourth week of treatment.

Survival curves in Figures 6a & 6b have been fit to illustrate the effect of above ground biomass on survival probability over time between light and shade treatments. Clearly, the amount of above ground biomass present at the start of treatment has a larger affect on survival probability in shaded treatments than in light treatments. In shaded treatments, survival probabilities change the most drastically between size categories in later weeks of treatment, ranging from negligible in the first three weeks to a decrease in survival probability from 0.73 to 0 between large and small sizes at the end of treatment (Figure 6). Meanwhile, the above ground biomass at the start of treatment in light conditions affects survival probability minimally between large and small samples by the end of treatment (Figure 6).

3.3 Testing Growth:

Growth is tested in the above ground experiment only. To examine the effect of patch identity, starting biomass (stem count), grazing and light treatment on growth, size change data \((N = 262; N = 262; n_A = 68, n_B = 69, n_C = 95, n_D = 30)\) from combined light treatments was fit to a logistic regression model with a binomial distribution such that growth (defined as any increase in above ground biomass over the duration of the experiment) is predicted by above ground biomass (stem count), patch identity, light treatment, and their interactions with grazing included as an additive term. Stepwise AIC evaluation retains above ground biomass (stem count), patch
identity, light treatment, grazing treatment, and the interaction between aboveground biomass and patch identity as useful predictors of growth (Table 7). Analysis of deviance of both the full (AIC=126.23) and the best supported models (AIC = 116.23) reveal both light ($p < 0.0001$) and grazing ($p < 0.0001$) explain the most model deviance. Additionally, the interaction between above ground biomass and patch identity ($p = 0.029$) is also determined to be relevant (Table 7).

Figure 7 illustrates for each treatment combination of light and grazing, variation in size change where size change is defined as difference between the log transformation of stem count at the beginning and end of treatment. Clearly, the largest amount of variation in size change occurs in samples exposed to grazing under lit conditions, while the smallest amount of variation occurs in un-grazed samples in lit conditions. Samples exposed to shade treatments experienced the largest decreases in size, and have similar means between grazed and un-grazed treatments. The presence of growth in light treatments, especially in un-grazed samples, in comparison with substantial loss of mass seen in shade treatments can be seen in Figure 8.
Figure 2. Rhizome Length and Mass. Emergent (•) and non-emergent (Δ) samples by light treatment (light or shade). \( N_{\text{light}} = 90, N_{\text{shade}} = 90. \)
Table 1 Analysis of Deviance (Type II) for Emergence AFT models of Combined Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Combined Light Treatments</th>
<th>Full Model AIC = 154.611</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome Mass</td>
<td>0.026</td>
<td>0.156</td>
</tr>
<tr>
<td>Rhizome Length</td>
<td>0.021</td>
<td>0.205</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.025</td>
<td>0.395</td>
</tr>
<tr>
<td>Light</td>
<td>0.208</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length</td>
<td>0.006</td>
<td>0.512</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID</td>
<td>0.045</td>
<td>0.185</td>
</tr>
<tr>
<td>Rhizome Mass: Light</td>
<td>0.083</td>
<td>0.012</td>
</tr>
<tr>
<td>Rhizome Length: Patch ID</td>
<td>0.016</td>
<td>0.553</td>
</tr>
<tr>
<td>Rhizome Length: Light</td>
<td>0.032</td>
<td>0.121</td>
</tr>
<tr>
<td>Patch ID: Light</td>
<td>0.016</td>
<td>0.555</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID</td>
<td>0.042</td>
<td>0.207</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Light</td>
<td>0.001</td>
<td>0.744</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID: Light</td>
<td>0.081</td>
<td>0.048</td>
</tr>
<tr>
<td>Rhizome Length:Patch ID: Light</td>
<td>0.058</td>
<td>0.111</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID:Light</td>
<td>0.341</td>
<td>&lt;&lt; 0.0001</td>
</tr>
</tbody>
</table>

** (Loglogistic distribution) Emergent samples only are represented, \( N_{\text{emerged}} = 72; \ n_A = 42, n_B = 17, n_C = 13. FM denotes full model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.
Table 2. Analysis of Deviance (Type II) for Emergence Logistic Regression Models of Segregated Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Light Treatments</th>
<th>Shade Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 107.42</td>
<td>BS AIC = 97.92</td>
</tr>
<tr>
<td></td>
<td>DEV</td>
<td>P</td>
</tr>
<tr>
<td>Rhizome Mass</td>
<td>0.001</td>
<td>0.86</td>
</tr>
<tr>
<td>Rhizome Length</td>
<td>0.572</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.216</td>
<td>0.037</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length</td>
<td>0.015</td>
<td>0.506</td>
</tr>
<tr>
<td>Rhizome Length: Patch ID</td>
<td>0.011</td>
<td>0.841</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID</td>
<td>0.115</td>
<td>0.175</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID</td>
<td>0.070</td>
<td>0.343</td>
</tr>
</tbody>
</table>

** All samples are represented, segregated by light treatment ($N_{\text{Light}} = 90$, $N_{\text{Shade}} = 90$); where FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor and P its significance in a Type II analysis of deviance.
Figure 3. Probability of Emergence over Time. Emergent samples represented only such that $N_{\text{emerged}} = 72$; $n_A = 42$, $n_B = 17$, $n_C = 13$. AL = patch A (light), AS = patch A (shade), BL = patch B (light), CL = patch C (light), CS = patch C (shade).
Table 3.a Below Ground Biomass Experiment: Analysis of Deviance for Survival AFT models of Combined Light Treatments

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Combined Light Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 210.88</td>
</tr>
<tr>
<td>Rhizome Mass</td>
<td>DEV 0.001  P 0.799</td>
</tr>
<tr>
<td>Rhizome Length</td>
<td>0.014  0.274</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.147  0.002</td>
</tr>
<tr>
<td>Light</td>
<td>0.292  &lt;0.0001</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length</td>
<td>0.000  0.951</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID</td>
<td>0.058  0.091</td>
</tr>
<tr>
<td>Rhizome Mass: Light</td>
<td>0.075  0.012</td>
</tr>
<tr>
<td>Rhizome Length: Patch ID</td>
<td>0.035  0.233</td>
</tr>
<tr>
<td>Rhizome Length: Light</td>
<td>0.013  0.3</td>
</tr>
<tr>
<td>Patch ID: Light</td>
<td>0.099  0.016</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID</td>
<td>0.114  0.009</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Light</td>
<td>0.077  0.012</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID: Light</td>
<td>0.020  0.432</td>
</tr>
<tr>
<td>Rhizome Length:Patch ID: Light</td>
<td>0.027  0.324</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID:Light</td>
<td>0.029  0.302</td>
</tr>
</tbody>
</table>

** (Weibull distribution) Emergent samples only are represented, $N_{\text{emerged}} = 72$; $n_A = 42$, $n_B = 17$, $n_C = 13$. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.
Table 3.b Below Ground Biomass Experiment: Analysis of Deviance for Survival AFT models of Segregated Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Light Treatment</th>
<th>Shade Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM (BS) = 78.45</td>
<td>FM AIC = 133.48</td>
</tr>
<tr>
<td></td>
<td>BS AIC = 129.21</td>
<td></td>
</tr>
<tr>
<td>Rhizome Mass</td>
<td>DEV 0.258 P 0.006</td>
<td>DEV 0.043 P 0.295</td>
</tr>
<tr>
<td>Rhizome Length</td>
<td>DEV 0.005 P 0.704</td>
<td>DEV 0.126 P 0.074</td>
</tr>
<tr>
<td>Patch ID</td>
<td>DEV 0.137 P 0.134</td>
<td>DEV 0.431 P 0.004</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length</td>
<td>DEV 0.063 P 0.175</td>
<td>DEV 0.007 P 0.682</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID</td>
<td>DEV 0.065 P 0.386</td>
<td>DEV 0.122 P 0.213</td>
</tr>
<tr>
<td>Rhizome Length: Patch ID</td>
<td>DEV 0.192 P 0.058</td>
<td>DEV 0.156 P 0.137</td>
</tr>
<tr>
<td>Rhizome Mass: Rhizome Length: Patch ID</td>
<td>DEV 0.281 P 0.016</td>
<td>DEV 0.116 P 0.230</td>
</tr>
</tbody>
</table>

** All samples are represented, segregated by light treatment ($N_{Light} = 90$, $N_{Shade} = 90$); where FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor and P its significance in a Type II analysis of deviance.

Table 4. Below Ground Biomass Experiment: Analysis of Deviance (Type II) for Survival Logistic Regression Models of Segregated Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Light Treatment</th>
<th>Shade Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM (BS) AIC = 34.81</td>
<td>FM (BS) AIC = 50.38</td>
</tr>
<tr>
<td>Rhizome Length</td>
<td>DEV 0.001 P 0.895</td>
<td>DEV 0.019 P 0.602</td>
</tr>
<tr>
<td>Rhizome Mass</td>
<td>DEV 0.177 P 0.016</td>
<td>DEV 0.080 P 0.287</td>
</tr>
<tr>
<td>Patch ID</td>
<td>DEV 0.108 P 0.171</td>
<td>DEV 0.479 P 0.033</td>
</tr>
<tr>
<td>Rhizome Length: Rhizome Mass</td>
<td>DEV 0.037 P 0.271</td>
<td>DEV 0.024 P 0.555</td>
</tr>
<tr>
<td>Rhizome Length: Patch ID</td>
<td>DEV 0.130 P 0.119</td>
<td>DEV 0.066 P 0.624</td>
</tr>
<tr>
<td>Rhizome Mass: Patch ID</td>
<td>DEV 0.079 P 0.273</td>
<td>DEV 0.000 P 0.998</td>
</tr>
<tr>
<td>Rhizome Length: Rhizome Mass: Patch ID</td>
<td>DEV 0.468 P 0.0005</td>
<td>DEV 0.332 P 0.093</td>
</tr>
</tbody>
</table>

** All samples are represented, segregated by light treatment ($N_{Light} = 90$, $N_{Shade} = 90$); where FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor and P its significance in a Type II analysis of deviance.
Figure 4. Probability of Survival over Time by Patch Identity (Below Ground Biomass Experiment). Emergent samples represented only such that $N_{\text{emerg}} = 72$; $n_A = 42$, $n_B = 17$, $n_C = 13$. AL = patch A (light), AS = patch A (shade), BL = patch B (light), CL = patch C (light), CS = patch C (shade).
Table 5.a Above ground biomass experiment: Analysis of Deviance (Type II) for Survival AFT models of Combined Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Combined Light Treatments</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 511.615</td>
<td>BS AIC = 470.29</td>
<td></td>
</tr>
<tr>
<td></td>
<td>DEV</td>
<td>P</td>
<td>DEV</td>
</tr>
<tr>
<td>Above Ground Biomass</td>
<td>0.093</td>
<td>&lt;0.0001</td>
<td>0.103</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.005</td>
<td>0.777</td>
<td>0.005</td>
</tr>
<tr>
<td>Grazing</td>
<td>0.002</td>
<td>0.512</td>
<td>0.002</td>
</tr>
<tr>
<td>Light</td>
<td>0.691</td>
<td>&lt;&lt;0.0001</td>
<td>0.768</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID</td>
<td>0.046</td>
<td>0.096</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Grazing</td>
<td>0.014</td>
<td>0.191</td>
<td>0.021</td>
</tr>
<tr>
<td>Patch ID: Grazing</td>
<td>0.003</td>
<td>0.892</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Light</td>
<td>0.005</td>
<td>0.537</td>
<td>-</td>
</tr>
<tr>
<td>Patch ID: Light</td>
<td>0.086</td>
<td>0.0001</td>
<td>0.088</td>
</tr>
<tr>
<td>Grazing: Light</td>
<td>0.011</td>
<td>0.116</td>
<td>0.014</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Grazing</td>
<td>0.033</td>
<td>0.261</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Light</td>
<td>0.000</td>
<td>0.261</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Grazing: Light</td>
<td>0.012</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Patch ID: Grazing: Light</td>
<td>0.000</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Grazing: Light</td>
<td>0.000</td>
<td>1</td>
<td>-</td>
</tr>
</tbody>
</table>

** (Weibull distribution) All samples are represented, N = 262; n_A = 68, n_B = 69, n_C = 95, n_D = 30. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.
Table 5.b Above Ground Biomass Experiment: Analysis of Deviance (Type II) for Survival AFT models of Segregated Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Light Treatments</th>
<th>Shade Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 85.86</td>
<td>BS AIC = 50.87</td>
</tr>
<tr>
<td></td>
<td>FM AIC = 409.66</td>
<td>BS AIC = 396.22</td>
</tr>
<tr>
<td></td>
<td>DEV</td>
<td>P</td>
</tr>
<tr>
<td>Above Ground Biomass</td>
<td>0.072</td>
<td>0.514</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.720</td>
<td>0.004</td>
</tr>
<tr>
<td>Grazing</td>
<td>0.156</td>
<td>0.089</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID</td>
<td>0.000</td>
<td>1</td>
</tr>
<tr>
<td>Above Ground Biomass: Grazing</td>
<td>0.052</td>
<td>0.617</td>
</tr>
<tr>
<td>Patch ID: Grazing</td>
<td>0.000</td>
<td>1</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Grazing</td>
<td>0.000</td>
<td>1</td>
</tr>
</tbody>
</table>

** (Lognormal distribution) All samples are represented, N\text{light} = 106, N\text{shade} = 156. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.
Table 6.a Above ground biomass experiment: Analysis of Deviance (Type II) for Survival Logistic Regression models of Combined Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Combined Light Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 187.11</td>
</tr>
<tr>
<td></td>
<td>DEV P DEV P</td>
</tr>
<tr>
<td>Above Ground Biomass</td>
<td>0.154 &lt;0.0001 0.158 &lt;0.0001</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.040 0.032 0.040 0.034</td>
</tr>
<tr>
<td>Grazing</td>
<td>0.742 &lt;&lt;0.0001 0.720 &lt;&lt;0.0001</td>
</tr>
<tr>
<td>Light</td>
<td>0.001 0.623 - -</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID</td>
<td>0.017 0.288 - -</td>
</tr>
<tr>
<td>Above Ground Biomass: Light</td>
<td>0.006 0.262 - -</td>
</tr>
<tr>
<td>Patch ID: Light</td>
<td>0.040 0.033 0.081 &lt;0.0001</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Light</td>
<td>0.000 1 - -</td>
</tr>
</tbody>
</table>

** All samples are represented, N = 262; n_A = 68, n_B = 69, n_C = 95, n_D = 30. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.

Table 6.b Above ground biomass experiment: Analysis of Deviance (Type II) for Survival Logistic Regression models of Segregated Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
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<th>Shade Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 38.88</td>
<td>BS AIC = 32.89</td>
</tr>
<tr>
<td></td>
<td>DEV P DEV P</td>
<td>DEV P DEV P</td>
</tr>
<tr>
<td>Above Ground Biomass</td>
<td>0.202 0.046 0.202 0.046 0.635 &lt;0.0001</td>
<td>0.688 &lt;0.0001</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.657 0.005 0.657 0.005 0.286 0.003 0.312 0.003</td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>0.142 0.094 0.142 0.094 0.000 0.884 - -</td>
<td></td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID</td>
<td>0.000 1 - -</td>
<td>0.078 0.291 - -</td>
</tr>
</tbody>
</table>

** All samples are represented, N_light = 106, N_shade = 156. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.
Figure 5. Probability of Survival over Time by Patch Identity (Above Ground Biomass Experiment) All samples are represented, N = 262; n_A = 68, n_B = 69, n_C = 95, n_D = 30. AL = patch A (light), AS = patch A (shade), BL = patch B (light), CL = patch C (light), CS = patch C (shade), DL = patch D (light), DS = patch D (shade).
Figure 6. Probability of Survival over Time by Above Ground Biomass in Light and Shade. Light treatments (Left), Shade treatments (Right). All surviving samples are represented, N=149. LG = large, Med = medium, Sm = small. ** Note the difference in scale between the Light treatments and Shade treatments.
Table 7. Analysis of Deviance for Growth Logistic Regression Models for Combined Light Treatments.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Combined Light Treatments</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FM AIC = 126.23</td>
<td>BS AIC = 116.23</td>
<td></td>
</tr>
<tr>
<td></td>
<td>DEV</td>
<td>P</td>
<td>DEV</td>
</tr>
<tr>
<td>Above Ground Biomass</td>
<td>0.001</td>
<td>0.788</td>
<td>0.001</td>
</tr>
<tr>
<td>Patch ID</td>
<td>0.021</td>
<td>0.775</td>
<td>0.021</td>
</tr>
<tr>
<td>Grazing</td>
<td>0.333</td>
<td>&lt;0.0001</td>
<td>0.333</td>
</tr>
<tr>
<td>Light</td>
<td>0.471</td>
<td>&lt;0.0001</td>
<td>0.471</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID</td>
<td>0.174</td>
<td>0.029</td>
<td>0.174</td>
</tr>
<tr>
<td>Above Ground Biomass: Light</td>
<td>0.000</td>
<td>0.9</td>
<td>-</td>
</tr>
<tr>
<td>Patch ID: Light</td>
<td>0.000</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Above Ground Biomass: Patch ID: Light</td>
<td>0.000</td>
<td>1</td>
<td>-</td>
</tr>
</tbody>
</table>

** All samples are represented, N = 262; n_a = 68, n_b = 69, n_c = 95, n_d = 30. FM denotes full model and BS denotes the best supported model, DEV is proportional model deviance explained by the predictor, and P its significance in a Type II analysis of deviance.

Figure 7. Variation in Size Change of Above Ground Biomass. All samples are represented, N = 262. Change in size is determined by the difference between the log transformed stem count at the beginning and end of treatment (5 week period).
Figure 8. Relative Growth Rate by Treatment. All surviving samples represented, non-grazed (Δ) and grazed (●).
4.0 Discussion:

The purpose of this study was to ask whether variation in response to stress occurs, and if so, to identify how this variation depends on factors such as patch identity, rhizome characteristics, and above ground biomass. To do so, we imposed several types of stress including light manipulation. Since the effect of light on emergence and survival in *Imperata cylindrica* has been previously studied (Paul & Elmore 1984; Patterson 1980; Gaffney 1996; Ramsey et al. 2003; Holm et al. 1977; MacDicken et al. 1997; Ramsey et al. 2003; Eussen 1977; Moosavi-Nia & Dore, 1979), our interest was to examine variability in responses to light (and other forms of) stress. Insight on variability in stress responses is facilitated by parsing the data into light treatments for analysis, partly because it allows for the decomposition of common (and frustrating) higher order interaction effects containing light.

4.1 Patch Identity:

Without exception, patch identity emerges as an important predictor of response when testing the probability of, and timing of emergence and death. In general, patch identity plays a greater role in explaining variation in shaded treatments than in light treatments. (Table 2, Table 3b, Table 4, Table 5b, Table 6b, and Table 8).
Time-to-event (AFT) models reveal strong relationships between patch identity and both time-to-emergence and time-to-death, indicating two individuals experiencing the same level of stress may respond differently. Survival curves show the same ranked survival probabilities between patch identities in both experiments, specifically in shaded conditions (Figure 4, Figure 5). Samples from patch A rank highest among patches (prob(survival) = 0.45, prob(survival)=0.471), followed by patch C (prob(survival)= 0.3, prob(survival)=0.31), and lastly patch B (prob(survival)=0, prob(survival)= 0.18). This repetitive ranking of patches between experiments in the decline in survival probability over time suggests that the rate of decline amongst patch identities differs predictably.

Only in the case of emergence does patch identity play a larger role in explaining variation in light rather than shade treatments. Emergence probability varies widely by patch identity in light treatments, while being reduced to 0 after the second week in shaded treatments, regardless of patch identity. In this case, the total amount of stress experienced by shaded samples (exposure to low light levels in combination with a complete removal of above ground biomass) likely overrode any detectable effect patch identity would have. Nevertheless, this experiment provides a unique view on how patch identity affects recovery rates in lighted treatments by revealing an obvious difference in emergence rates between patch identities. This means that patch identity not only influences the short-term response to stress resulting in life or death, but that it also has lasting impacts on recovery in survivors. Interestingly, this experiment ranked emergence success between
patch identities similarly to that of survival ranks discussed earlier. Samples from patch A emerge more slowly and continuously throughout the experiment, resulting in the highest emergence potential by the end of treatment, followed by patch B, and lastly patch C (Figure 2). If this indicates that some patch identities may be hardier than others in multiple scenarios is unclear.

What accounts for this variation in emergence, survival and growth capacities among patch identities is unclear. It may be due to a number of factors, be they genetic, environmental, or their interaction. Assume for a moment that all patches tested here are genetically identical, that is to say each patch represents a different ramet of the same genet. Phenotypic plasticity arising from variation in local environmental factors, would then explain the patch-level differences. For example, Patch X is located under an open canopy such that light availability is high, while Patch Y is located under a tree line with less light availability than Patch X. Patch X can produce and store more photosynthate and carbohydrates than Patch Y, and as such can devote more resources to growth, flowering, and seed production than patch Y. These developmental differences can result in varying capacities or traits concerning survivorship, emergence or growth between ramets when exposed to stress.

Assume now that patches are in fact not genetically identical, but that each patch is a unique genotype, or that a gradient of genetic similarity exists between patches. It may be that some patches share one parent, while others do not. Differences in survivorship and other life history traits
may arise strictly from genetic differences between patches, from environmental differences between patches acting in the same way on all genotypes, or from genotype-environmental interactions in either the present or the previous generation. Take for example, two patches arisen from seed produced by one source of pollen and two maternal sources, one of which is exposed to stress during seed development. Seeds produced by a stressed maternal source may receive fewer nutrients during development, with effects on survival and other life history traits throughout those individuals’ lives.

We have shown that there is substantial variation among patches here. Other clonal grasses have been shown to display substantial within-population genetic variation (Capo-chichi et al. 2005; McCormick et al. 2009; Bryson & Carter 1993; Bush 2007). The extent to which genes, environment, or their interaction each contribute to the phenotypic variation we have documented is a matter for future investigation.

If there is a genetic component to this variation, control efforts may lead to an evolutionary response by *I. cylindrica* populations. Whether natural selection moves towards a few more resilient genotypes, or towards dominance of different genotypes in different microenvironments, depends on the scale of gene flow with respect to the patchiness of the environment. At the very least, results from this experiment warrant further examination into the possibility that heterogeneous responses to stressful conditions result in varied survival rates, and as such may have important impacts on
population processes such as maintenance and expansion, and thence on control efforts.

4.2 Rhizome Characteristics:

In this study, both rhizome length and mass were found to be important to emergence and survival capacities. Rhizome length is likely important to emergence because of the presence of nodes along the rhizome. Nodes contain apical meristems from which new shoots emerge (Watson, 1986). Thus longer rhizomes, on average, increase the number of available nodes for shoots to emerge, yielding higher emergence potential. One previous study found that node number and internodal length did not impact probability of emergence in *Imperata cylindrica* (Soerjani 1970), while another found that rhizome regeneration was linked with rhizome length (Ayeni & Duke 1985). Clearly, rhizome length plays an important role in emergence in this experiment (Table 2).

Although rhizome mass does not play a detectable role in emergence in lighted conditions in this study, it is important under shaded conditions (Table 2). It may be that non-structural carbohydrates stored in the internodal regions of the rhizome are relied on more heavily in sustaining vitality during growth in unfavorable conditions. Moosavi & Dore (1979) found that under six weeks of intense shade treatment, shoot and rhizome dry weights were significantly adversely affected, causing a shift from low to extremely high shoot-to-rhizome ratios, which they attributed to exhaustion of non-structural carbohydrate resources.
Though both rhizome mass and length are important in explaining variation in survival, their relative contributions differ. Rhizome length is important in predicting time-to-death in shade treatments (Table 3b). On the other hand, rhizome mass plays a detectable role only for survival in light treatments, as indicated by both logistic regression and time-to-death (AFT) models (Table 3b, Table 4).

4.3 Above Ground Biomass:

Above-ground biomass plays a key role in survival. One might expect this, as small individuals are less likely to survive than larger ones, especially under stressful conditions. Fewer stems and leaves in smaller plants result in lesser photosynthetic ability, as well as a decreased ability to withstand and recover from loss of mass when compared to individuals with larger amounts of above ground biomass. This study shows an intensification of survival dependency upon above ground biomass when subjected to stress. The combination of starting size and stressful conditions is seen to decrease survival chances more quickly in smaller samples than in larger samples, as seen in Figure 6.

Logistic regression reveals that above ground biomass plays a much stronger role in determining survival in shaded treatments than in light treatments. This again makes biological sense, in that the larger individuals are expected to have greater survival chances than smaller individuals, especially under stressful conditions. Above ground biomass is also important with respect to growth (Table 7).
4.4 Grazing:

In this study, the amount of growth was largely determined by the presence or absence of grazing. Growth observed in un-grazed samples under lighted treatment far exceeds that of all other treatments (Figure 7, Figure 8). This suggests that mowing or grazing may help control *Imperata cylindrica* populations. Mowing is often a popular localized control methodology in resource-poor regions where infestation poses large problems, such as the South Pacific and Southeast Asia. It should be noted that grazing or mowing efforts alone produce less than ‘acceptable’ (> 80 %) levels of control based on rhizome biomass reduction. Consequently, it is likely that control can best be achieved from combinations of mowing, grazing and/or discing with other control methods (Willard et al. 1996). We found no evidence for ‘compensatory growth’ (McNaughton 1983), which is sometimes suggested as an explanation for weedy plants being unaffected by defoliation.

Grazing also influences survival, though more strongly in light treatments than in shade (Table 5b, Table 6b). Because all samples were ‘grazed’ at the beginning of this experiment, we can make no distinction on how the timing of grazing affects survival probability.
Table 8. Results Summary: Relevant Model Terms.

<table>
<thead>
<tr>
<th>Exp.</th>
<th>Predictor</th>
<th>Emergence</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Light</td>
<td>Shade</td>
</tr>
<tr>
<td>Below Ground Biomass Experiment</td>
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</tr>
<tr>
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<td>AFT</td>
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<tr>
<td></td>
<td>Rhizome Length</td>
<td>LG</td>
<td>LG</td>
</tr>
<tr>
<td></td>
<td>Light</td>
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<tr>
<td></td>
<td>Rhizome Mass: Patch ID</td>
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</tr>
<tr>
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<td>Rhizome Mass: Light</td>
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<td>Rhizome Length: Patch ID</td>
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<table>
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<th>Survival</th>
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<td>Grazing</td>
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<td>Above Ground Biomass: Patch ID: Light</td>
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<td>AFT</td>
</tr>
</tbody>
</table>

** Best supported models only. LG = logistic regression model with binomial distribution, AFT = accelerated failure time model with best fit distributions. Bold indicates a statistically significant p value.
5.0 Implications for Management:

Life history traits such as growth, survival, and clonality determine how populations grow, spread, or decline (Gurevitch et al. 2011). Control efforts undoubtedly affect invasive populations by altering vital rates such as survival and reproduction, though not necessarily in the way we hope.

Because heterogeneous responses to stressful conditions (like those imposed by control efforts) often result in varied demographic parameters (i.e. survival rates) instead of local extinction, they are likely to have important impacts on population growth. Evolutionary adaptation to control efforts may take a number of different forms – adaptation to the conditions experienced by “average individuals” in the population, adaptation to different microsites, or adaptation to the unpredictability of the environment. Evolutionary change, in turn, may directly affect the demography of the invasive population, or alter organisms’ physiological and morphological traits, again leading indirectly to demographic change (Gurevitch et al. 2011). This cycle of evolutionary and demographic change driven by variation in survival resulting from control efforts may play a major role in the future of communities impacted by invasive species. Recent work reveals that heterogeneous survival in long-lived species can increase the long-term growth rates in populations of any size. The increase occurs because the population becomes increasingly dominated by the more robust individuals.
Accordingly, control efforts must begin to address variation in response to treatment.

Assume for a moment, that the variation in this study has a purely genetic basis. If some genotypes perform better under different environmental conditions or respond differently to stress, implications for control efforts may be severe. Ineffectively applied or maintained control efforts, especially when used alone, may drive the selection of more resistant and resilient genotypes. On the other hand, if the variation we have documented is purely phenotypic, it suggests that, at least in this study population, *I. cylindrica* is remarkably plastic, and this too must be accounted for in control efforts. How this particular issue should be addressed by control agencies is a matter of practicality. Two major points are apparent. First, although monetary and staffing limitations often restrict the time and methods used in eradication efforts, regular observation of site-specific control method efficacy and varied combinations of control methods stand to be the most effective at reducing heterogeneous survival capacities within a population and as such, can help avoid the selection of increasingly robust genotypes.

Second, the common practice of mowing as part of a control strategy seems prudent and effective, but its use comes with added responsibility. Most agencies involved in control efforts operate at regional scales such as the county, district, or state level. Agencies tend to oversee the control of multiple local populations of varying sizes. Plant material, including rhizome pieces, often builds up along the sides and undersides of mowers and
landscape equipment used by control agencies. These materials picked up at one location, can be transported long distances and deposited in other local *I. cylindrica* populations. Such shared use of equipment over multiple local or regional populations can facilitate the spread of genotypic diversity, with potentially large impacts on responses to selection and on population growth rates. To avoid the spread of genotypic diversity across regional scales, equipment used by control agencies should be thoroughly disinfected between uses across different sites.

Heterogeneity in stress response can have important consequences. It can contribute to both growth rates and selection responses of local populations. The movement of plant material between local populations (during control efforts) may inadvertently contribute to gene flow, with potential effects on local growth rate and long-term selection response. Our results warrant further study of heterogeneous responses to stressful conditions as this heterogeneity may have important impacts on population processes such as maintenance and expansion, as well as on evolutionary adaptation to control efforts.
List of References:


Appendices:
Appendix A. Additional Figures:

Figure A1. Sample Processing. Rhizome pieces with attached blades and stems are potted up and allowed to recover for 9 weeks.
Figure A2. Below Ground Biomass Experiment Set Up. Lighted treatments (left) and shaded treatments (right). All treatments were located against the southern face of the Fox Greenhouse, at the University of South Florida Botanical Gardens.
Figure A3. Above Ground Biomass Experiment Set Up. Lighted Treatments shown only. All treatments were located in the Fox Laboratory at the University of South Florida Science Center.
About the Author:

Sarah Grace Sanford was born in Buffalo, New York where she resided until her attendance at the University of South Florida. There she first obtained a Bachelors of Science in Environmental Science and Policy. During her undergraduate studies, she conducted geologic research under the watchful supervision of Dr. Rich Oches and Dr. Peter Harries. Her work in this area included the use of novel multivariate statistical analyses in order to resolve aminostratigraphic investigations of fossiliferous marine high-stand deposits in Florida that are hindered by reduced temporal resolution when distinguishing stratigraphic units on the basis of amino acid D/L ratios.

After the completion of her Bachelors, she continued academic pursuits at the University of South Florida, this time under the tutelage of Dr. Gordon Fox. Here, her research efforts were directed towards understanding the ecology of invasive species and the unanticipated impacts control efforts may have. Her work has since been presented at multiple regional and national conferences.

At the conclusion of her graduate studies, Sarah gave birth to her and her husband’s first child, Grace. Aside from that new adventure, she plans on entering the private sector before returning to academics sometime in the future.