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Conditions Responsible For The Success Of Carnivorous Plants In Nutrient-Poor Wetlands

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CONDITIONS RESPONSIBLE FOR THE SUCCESS OF CARNIVOROUS PLANTS IN

NUTRIENT-POOR WETLANDS

A Dissertation
presented in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in the Department of Biology
The University of Mississippi

by

Matthew J. Abbott

ABSTRACT

Despite the vast array of past research focused on carnivorous plants, few studies have investigated the ecological interactions between carnivorous and non-carnivorous plant species. I addressed the following three questions: (1) Does niche complementarity promote coexistence between fire-adapted carnivorous and non-carnivorous species? (2) Do carnivorous plants rely on both leaf traps and arbuscular mycorrhizal fungi to access different nutrients that are in high demand after fire in nutrient poor bogs? (3) Why are carnivorous plants largely absent from nutrient-rich wetlands? I addressed the first question by examining the three-way interacting effects of fire, prey-derived nutrient availability, and root competition from neighbors on *Sarracenia alata* growth. I found no evidence of belowground competition on growth, nor did belowground competition interact with fire to influence growth. To address the second question, I used carnivorous *Drosera tracyi* to experimentally test the effects of light availability and the availability of nutrients found in higher concentrations in prey versus nutrients found in higher concentrations in post-fire ash on relative investment in carnivory versus AMF colonization. Although the addition of phosphorus and other nutrients besides nitrogen appeared to slightly reduce investment in carnivory, I found no effect of late season fire on carnivory or AMF colonization in *D. tracyi*. To address the third question, I compared the performance of *S. alata* in a nutrient-rich marsh and a nutrient-poor bog, with and without neighbors. I also measured multiple soil characteristics potentially responsible for transplant performance. I found no evidence of competition from neighboring plants on *S. alata* growing in either the nutrient rich marsh or the nutrient-poor bog. Rather, I found that *S. alata* were intolerant of the low oxygen

levels within the nutrient-rich marsh soils. Together, these results suggest interspecific competition between non-carnivorous and carnivorous plants may be weak in the wet pine savannas studied here. I suggest that the ability of a large number of species to tolerate the abiotic conditions present in wet pine savannas, combined with weak resource competition among herbaceous plants (carnivorous and non-carnivorous) enables species coexistence in these uniquely diverse ecosystems.

DEDICATION

This work is dedicated to my wife, Megan, and to our daughter, Teresa Clare (due May 31, 2017).

LIST OF ABBREVIATIONS

FMNNC   Fire-mediated nutrient niche complementarity

FMCR   Fire-mediated competitive release

NNC   Nutrient-niche complementarity

RGR   Relative growth rate

N   Nitrogen

P   Phosphorus

K   Potassium

Mg   Magnesium

AMF   Arbuscular mycorrhizal fungi

LAI   Leaf area index

ppt   Parts per thousand

mV   Millivolt

ACKNOWLEDGMENTS

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NICHES ON COEXISTENCE OF A CARNIVOROUS PITCHER PLANT AND ITS NON-

CARNIVOROUS NEIGHBORS

ABSTRACT

Disturbance- and niche-centered theories for species coexistence have generally been treated as mutually-exclusive explanations for high diversity in pine savannas of the southeastern United States; however, their potential interdependence had not been tested until now. The pale pitcher plant (*Sarracenia alata*) is an ideal model organism to test the potential interacting effects of these drivers because it is adapted to frequent disturbance (i.e., fire), and its apparent nutrient-niche (i.e., captured prey via modified leaf traps) can be easily manipulated. Using a full factorial design, I examined the three-way interacting effects of simulated fire (clipping and fertilization), prey-derived nutrient availability (starvation), and root competition from neighbors (trenching) on *S. alata* growth and investment in leaf traps in order to test three different competition-based hypotheses for species coexistence: fire-mediated nutrient niche complementarity (FMNNC), fire-mediated competitive release (FMCR), and nutrient-niche complementarity (NNC). My results provided no support for the FMNNC, the FMCR, or the NNC hypotheses. However, I did find that *S. alata* responded to light-mediated increases in nitrogen limitation following simulated fire and reduced access to prey by increasing investment in open pitchers. My results therefore suggest that increases in light and nutrients other than nitrogen associated with fire could result in increased prey-derived nitrogen limitation of *S. alata* growth without increasing belowground competition for nutrients. I discuss several potential reasons why belowground competition was not detected in the current study.

INTRODUCTION

Botanical carnivory is a unique trait among plants in that it allows the plants to capture and digest prey through their leaves and thus supplement their supply of underground nutrient resources. This trait had been widely assumed to enable carnivorous plants to avoid competitive displacement by non-carnivorous species through nutrient-niche complementarity, but rarely has this assumption been tested (Brewer 2003a). Interestingly, contrary to predictions, previous work found that, only when neighbors were removed and light was no longer limiting, did the pitcher plants (*Sarracenia alata*) respond to the prey exclusion treatments, suggesting that the demand for nutrients (including soil nutrients) was low when light was limiting. In general, belowground competition in plants tends to be greater when light is not limiting to growth (Coomes and Grubb 2000). Hence, carnivory might still be an important mechanism for avoiding competitive displacement by non-carnivorous plants when light is no longer limiting. When not shaded, carnivorous plants that are denied prey could be placed at a competitive disadvantage because of their reduced root systems compared to non-carnivorous plants (Brewer 2003a; Adlassnig et al. 2005) and/or because of reduced soil nutrient uptake by roots that results from being denied prey (Adamec 2002). In order to test the hypothesis that carnivorous plants that are denied prey are more vulnerable to root competition when light is not limiting, it is necessary to examine the three-way interaction between light availability, access to prey, and root competition. If carnivory is a means by which plants can avoid competitive suppression by non-carnivorous plants when light is not limiting, then access to prey should be most beneficial to carnivorous plant growth when (1) light is not limiting (Givnish et al. 1984) and (2) carnivorous plants are subjected to belowground competition with their non-carnivorous neighbors (Brewer 2003a).

Understanding the interactions between light, prey access, and belowground competition could elucidate the factors influencing coexistence of carnivorous and non-carnivorous plants in pine savannas. Pine savannas are characterized by a relatively sparse overstory canopy dominated by *Pinus palustris* and/or *Pinus elliottii* and an understory composed of a highly diverse assemblage of herbaceous plant species, including both carnivorous and non-carnivorous species (ref. Walker and Peet 1983; Peet and Allard 1993; Palmquist et al. 2014). It remains unclear whether the coexistence of carnivorous and non-carnivorous species characteristic of pine savannas is the result of fire (Grime 1973, 1979; Connell 1978; Huston 1979; Glitzenstein et al. 2003), niche complementarity (Newman 1973; Tilman and Pacala 1993), some combination of both (Walker and Peet 1983; Brewer 2006), or stochastic processes and competitive equivalence (Hubbell 2001; Myers and Harms 2009). Pine savannas are comprised of fire-adapted species that are rooted in nutrient poor soils. Frequent low-intensity disturbances (e.g., fires) combined with low rates of competitive displacement in nutrient-poor soils therefore could be important in promoting species coexistence (Huston 1979; Walker and Peet 1983; Glitzenstein et al. 2003). Carnivorous plants in particular have been hypothesized to depend greatly upon fire for persistence and to be vulnerable to competitive displacement in the absence of fire (Gibson 1983; Juniper et al. 1989; Givnish 1989), and studies have shown that some species indeed benefit from fire (Roberts and Oosting 1958; Kessler et al. 2008; Paniw et al. 2015; Paniw et al. 2016). On the other hand, carnivorous plants may not be at a competitive advantage to non-carnivorous plants in pine savannas because carnivory represents one of many complementary adaptations for tolerating nutrient-poor soils (e.g., nitrogen fixation and the full complement of mycorrhizal associations – arbuscular, ectomycorrhizal, heath-associated, orchid-associated, myco-heterotrophy). In addition, different species of co-occurring plants produce

roots that differ in their vertical and horizontal extent, allowing for the occupation of different niche spaces (Stubbs and Wilson 2004). Hence, the wide variety of niches for nutrient acquisition could contribute to the high diversity of plant species observed in pine savannas. Determining which hypothesis or combinations of hypotheses best explain the coexistence of carnivorous and non-carnivorous plants will require experimental manipulation of disturbance regimes, nutrient availability, and niches. Finally, although some species clearly are competitively superior to others in pine savannas (e.g., trees and shrubs versus herbs), some researchers have suggested that dispersal limitation and competitive equivalence among herbaceous species, irrespective of differences in nutrient acquisition or phenology, may be sufficient to promote coexistence of herbs not subjected to competition from woody plants (Myers and Harms 2009; Brewer in press).

Disturbance-centered and niche-centered theories have generally been treated as mutually-exclusive explanations of species coexistence. Brewer (2006) proposed, however, that disturbances and niche differences might not be independent drivers of species coexistence in pine savannas. Light and nutrients both limit growth in pine savannas, and competition for these resources could be mediated by the interaction of fire and interspecific differences in the ways in which nutrients are acquired. Consequently, competition for light could be most important during years without fire and competition for nutrients most important during years with fire.

In this study, I tested the general hypothesis that fire (or other predominantly aboveground disturbances that increase light) interacts with nutrient niche complementarity to influence coexistence of a carnivorous pitcher plant and its neighbors. Fire potentially reduces competition for light by reducing aboveground biomass; however, because most pine savanna plants are adapted for surviving fire, fire does not represent a significant disturbance to

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belowground portions of pine savanna plants and therefore is not likely to reduce belowground competition. Instead, increased light levels following fire may actually increase growth, which in turn could increase belowground competition for nutrients. Nutrient niche complementarity may represent a mechanism by which nutrient competition could be reduced following fire. On the other hand, if fire simply increases both light and the availability of limiting nutrients, then fire, alone, may reduce competition overall.

In this study, I tested the following alternative hypotheses: (1) Fire-mediated nutrient-niche complementarity (FMNNC) – competition for light and nutrients is mediated by the interaction of fire and interspecific differences in nutrient uptake such that the potential for increased belowground competition for nutrients is increased after fire, but plant carnivory becomes an effective strategy for avoiding root competition after fire (nutrient niche complementarity); (2) Fire-Mediated Competitive Release (FMCR) – fire reduces aboveground competition and may or may not increase nutrient limitation of growth, but it does not increase below ground competition for nutrients, and (3) Nutrient-Niche Complementarity (NNC) – prey exclusion exacerbates the effect of root competition, with or without fire. The pale pitcher plant (i.e. *Sarracenia alata*) is an ideal focal species for testing these alternative hypotheses because its primary nutrient source (captured prey) can easily be manipulated by simply plugging its pitchers.

METHODS

Location

This study was conducted in open wet pine savannas in Desoto National Forest (30°43' N, 88°58' W) and in Grand Bay National Estuary Research Reserve (30°27' N, 88°25' W). These two sites are similar in that they are both dominated by *Pinus elliottii* in the overstory, they contain poorly drained, low pH soils, and they have both been historically maintained by regular fires. The two sites differ, however, in that the understory in the Grand Bay NERR site is dominated by *Aristida stricta*, while the understory in the Desoto NF site is dominated mostly by *Ctenium aromaticum* and *Muhlenbergia expansa.*

Experimental Setup

During the summer of 2013, forty 1 m^2 plots were established in wet pine savanna at both Grand Bay NERR and Desoto NF. The plots were centered on at least one ramet of *Sarracenia alata* each and initial species composition was recorded (described below). In the spring of 2014, at the beginning of fire season, half of the plots at each site were randomly chosen to receive prey exclusion treatments in the target pitcher plants. Prey was excluded from the selected plants by inserting cotton plugs into the bottoms of the pitchers so that the absorptive zones of the pitchers were blocked. All new pitchers that sprouted throughout the duration of the experiment received cotton plugs as soon as they matured and hardened. In addition to the prey exclusion treatments, half of the plots that received the exclusion treatments and half of the plots that did not were randomly chosen to receive trenching treatments in order to reduce root competition with the target pitcher plants' neighbors. The trenching treatments were accomplished by cutting 20 cm deep circles around the target pitcher plants (~10 cm radius) with a spade. The trenches

were re-cut monthly throughout the duration of the experiment. Next, half of the plots within each of the aforementioned treatment combinations were randomly chosen to receive simulated fire treatments. Fire was simulated in the randomly chosen plots by cutting and removing all above ground vegetation and spreading fertilizer. An aqueous fertilizer solution with nutrient concentrations of 250 ppm P; 190 ppm K; 30 ppm Mg, and 6 ppm Mn was added to each 1 m^2 plot to simulate the nutrient inputs that would normally accompany ash deposition (Gillon et al. 1995; Brewer, unpublished data). These fire simulation treatments were reapplied in the spring of 2015. Although actual fire treatments would have been ideal, strict fire regulations at the study sites prevented the use of prescribed fire in this experiment. Nevertheless, since light availability at the soil surface of pine savannas has been found to be the most important resource affected by fire disturbance (Brewer 1999a, 2003; Brewer et al. 2009), it was determined that clipping and fertilization would be an adequate alternative to real fire at my study sites. Preliminary observations have revealed that the ash produced by burning pine savanna vegetation contains elevated concentrations of phosphorus, potassium, magnesium, and manganese, but not nitrogen. In addition, studies that examined soil biochemistry in the top 5 cm immediately, or soon after fire, found increases in available P (Dean et al. 2015) or reduced phosphatase activity coupled with increased organic matter (suggesting increased P availability; Rietl and Jackson 2012). Although fire may increase nitrogen availability also (e.g., through increased mineralization rates, Hobbs and Schimel 1984, Kaye and Hart 1998, Dean et al. 2015), I predicted that the dramatic increases in light levels at the soil surface combined with greater rates of nitrogen volatilization relative to that of P or K (Christensen 1977; Gillon et al. 1995) and the addition of fertilizer that matched natural ash concentrations could lead to increased nitrogen-limitation of growth in pine savanna vegetation (Christensen 1993).

Data Collection

In the spring of 2013, immediately after plot establishment, species composition within a 0.09 m^2 subplot surrounding the target pitcher plant was recorded in each plot. The abundance of each neighboring species was given a ranking of 1 through 4. A species was given a "1" if there was only one individual, a "2" if there were between two and five individuals, a "3" if there were between 6 and 10 individuals, and a "4" if there were 11 or more individuals in the subplot. Using the composition data and the species' root length averages described in Brewer et al. (2011), weighted averages of neighbor root length were calculated in order to approximate potential belowground competition intensity.

In the spring of 2014, immediately before treatment application, initial groundcover canopy openness was measured with a LI-COR plant canopy analyzer (LI-COR Biosciences, Lincoln, NE), soil moisture levels were measured using an Aquaterr M-300 portable soil moisture meter (Aquaterr Instruments, Costa Mesa, CA), and the initial volume of the tallest pitcher of each target plant was determined by recording maximum diameter and height (minus the length of the support tissue (hereafter, the "petiole") of the pitcher and calculating the volume of a cone (Brewer 2003a). Relative investment in carnivory vs. shade avoidance was also calculated by dividing the pitcher volume of the tallest pitcher in each plant by the length of its petiole. Higher pitcher volume to petiole length ratios indicate that the plants are investing more resources into carnivory, while lower pitcher volume to petiole length ratios indicate that the plants are investing more resources into light capture (Brewer 2003a). These measurements were repeated at the end of the first growing season and at the conclusion of the experiment. In the fall of 2015, at the conclusion of the experiment, the entire pitcher plants were removed from the plots and live pitchers and belowground tissues were dried so as to measure final total biomass. To nondestructively estimate initial biomass, the final pitcher volumes were regressed against

final total dried biomass, the parameters for the line of best fit were obtained, and the initial

volumes were inserted into the equation so that initial biomass values for each plant could be

calculated. Together, the final weights and estimated initial weights were used to calculate

relative growth rates (Brewer 2003a). Note that initial volume of the largest pitcher was used to

estimate initial biomass because past research has shown it to be most strongly correlated with

total biomass (e.g., as opposed to total pitcher number; Brewer 2003a).

Data Analysis

A four-way ANCOVA (i.e. fire simulation x trenching x prey availability x site (type III

sums of squares)) was used to analyze differences in relative growth rate and pitcher volume to

petiole length ratios, using initial estimated biomass (log-transformed) as a covariate.

Environmental variables such as initial canopy openness, average soil moisture, weighted

averages of neighbor root length were investigated as possible covariates in the analyses, as was

dried prey necromass to pitcher volume ratio. Simple regressions of response variables corrected

for initial biomass with each of the aforementioned environmental variables revealed that none

were significant. All response data were log-transformed to better meet the ANOVA

assumptions of normality and homoscedasticity.

Predictions

The FMNNC hypothesis predicts that (1) the demand for nutrients and/or the benefit of

carnivory increases after simulated fire (Givnish et al. 1984; Brewer 2003a) and (2) as a result,

belowground competition from surrounding neighbors will have a greater effect on pitcher plants

that are denied prey material than on those that are not (a significant fire simulation x trenching x

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prey availability interaction; Figure 1a). The hypothesis also predicts that the magnitude of this interaction will be greatest in plots with relatively short pitchers and high weighted averages of neighbor root length. The FMCR hypothesis predicts that simulated fire will increase growth (a significant main effect of simulated fire; Figure 1b) and may interact with prey availability to influence growth such that prey exclusion reduces growth more after simulated fire (Figure 1c). The hypothesis does not predict, however, that there will be a three-way interaction between fire, prey availability, and trenching. Hence, an increase in light availability will not necessarily translate to increased competition for soil resources. The NNC hypothesis predicts that prey exclusion exacerbates the effect of root competition, with or without simulated fire (as indicated by a significant trenching x prey availability interaction; Figure 1d).

Finally, the lack of support for any of the three above hypotheses would indicate that coexistence of pitcher plants with their neighbors is the result of competitive/fitness equivalence (neutrality), positive interactions (Bertness and Callaway 1994), phenotypic plasticity in resource use (Brewer 1999b; Dybzinski and Tilman 2007) or requires trade-offs other than those examined here (e.g., dispersal, competition for water or space; Myers and Harms 2009; Brewer et al. 2011).
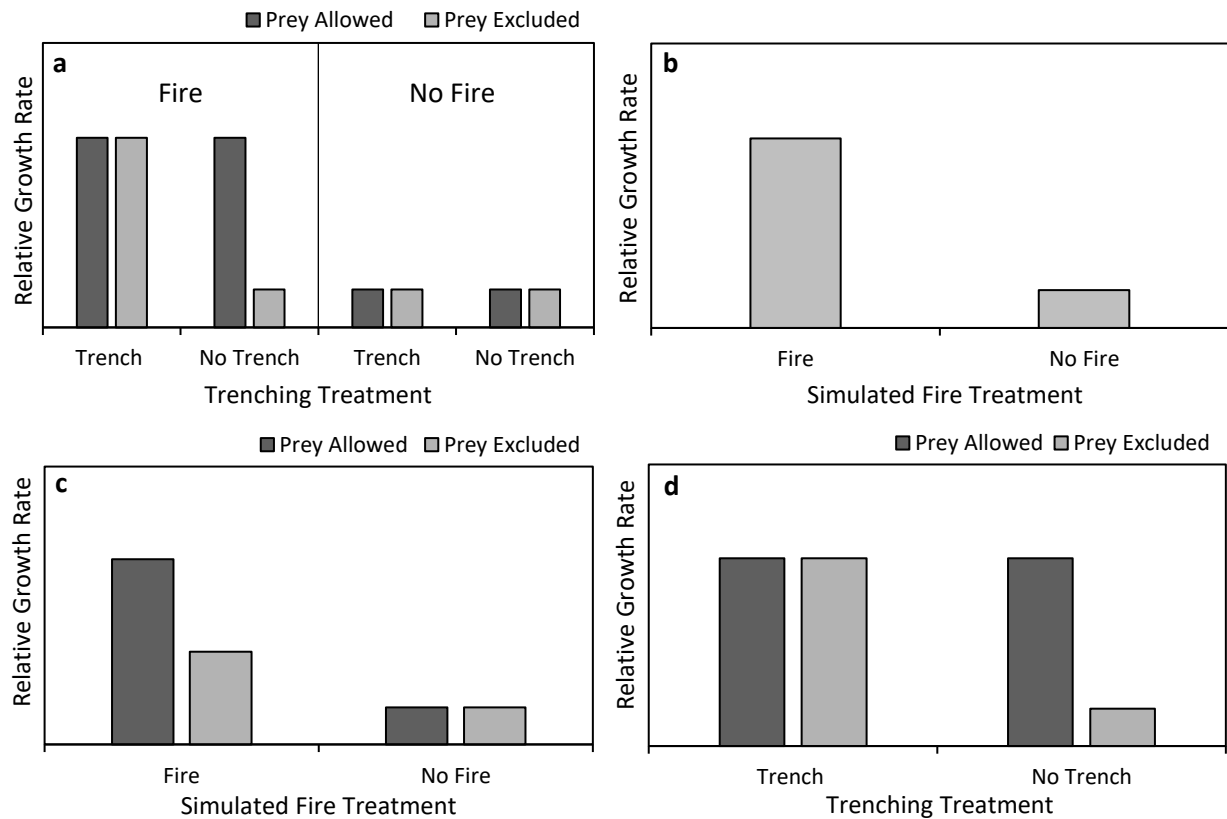
Figure 1: Bar graphs depicting predictions of research hypotheses: (a) fire-mediated nutrient-niche complementarity (FMNNC), (b) fire-mediated competitive release (FMCR), (c) fire-mediated competitive release and nutrient limitation following increased light availability, and (d) nutrient-niche complementarity (NNC) in pitcher plants in response to the different treatment combinations.

RESULTS

Growth Reponses to Treatments

Overall, my results provide no support for any of the niche or disturbance-based hypotheses of species coexistence. The three-way interaction between simulated fire, trenching, and starvation was not significant ($F_{1,58} = 2.265$, $p = 0.138$; Figure 2). Hence, simulated fire and starvation did not act together to increase belowground competition, as predicted by the fire-

mediated nutrient-niche complementarity hypothesis. Simulated fire did not result in increased

RGR relative to unclipped controls ($F_{1,58} = 2.526$, $p = 0.117$), and because the negative effect of

starvation was not exacerbated by simulated fire, as indicated by a lack of a two-way interaction

between simulated fire and prey exclusion ($F_{1,58} = 2.335$, $p = 0.132$), I found no evidence in

support of the cost-benefit model to explain the benefit of carnivory and thus evidence for fire-

mediated competitive release.
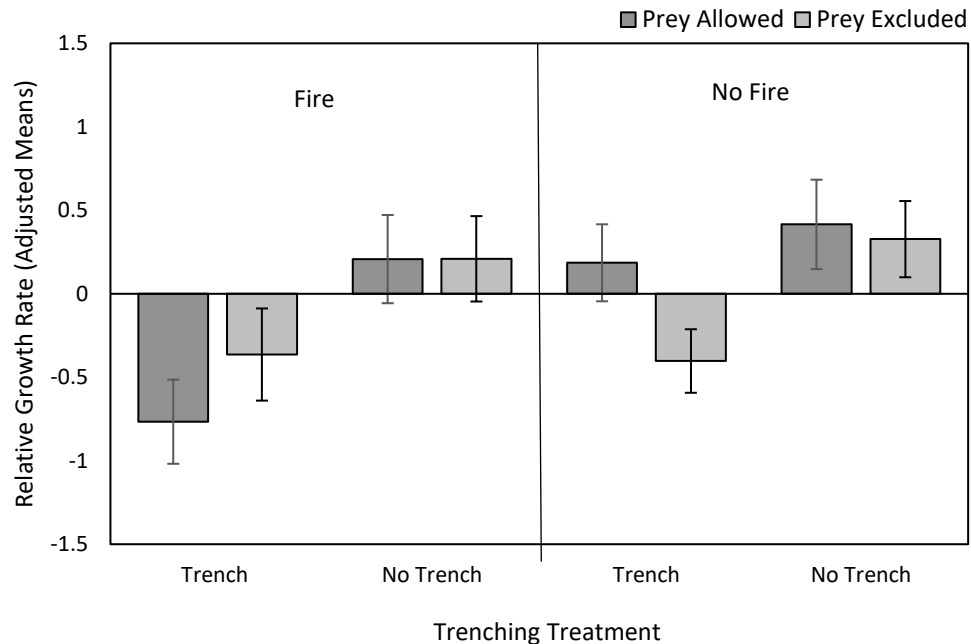
Figure 2: Effects of simulated fire, trenching, and starvation treatments on target pitcher plant relative growth rate (RGR). Error bars indicate ±1 standard error.

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There was no evidence that trenching reduced belowground competition, much less belowground competition for nutrients. There was no significant two-way interaction between trenching and starvation ($F_{1,58} = 0.006$, $p = 0.940$); therefore, starvation did not increase belowground competition for nutrients, as predicted by the nutrient-niche complementarity hypothesis. I found no positive effect of trenching on RGR, and in fact the main effect of trenching was negative ($F_{1,58} = 12.773$, $p < 0.001$). Later in the first growing season I realized that the rhizomes of multiple plants had been unknowingly severed by my trenching treatments, possibly reducing the resource reserves of the affected plants and stunting their growth. A significant trenching by site interaction revealed that this artifact was largely limited to the Desoto NF site ($F_{1,58} = 7.200$, $p = 0.009$; Figure 3), where the pitcher plant targets were significantly larger ($F_{1,72} = 21.07$, $p < 0.001$) and possessed rhizomes that were more likely to extend beyond the radius of the trenching area. When considering Grand Bay NERR alone (where rhizome severing was less frequent), the trenching treatments had neither a positive or negative effect on RGR ($F_{1,30} = 0.650$, $p = 0.426$). When considering all the untrenched plots across both sites, the clipping (i.e., simulated fire) treatment appeared to interact with the abundance of neighbors weighted by root length ($F_{1,31} = 3.901$, $p = 0.057$; Figure 4); however, RGR was negatively correlated with neighbor root length in the unclipped control plots ($r^2 = 0.308$), not in the clipped plots ($r^2 = 0.004$). No other interactions were significant (prey availability x neighbor roots: $F_{1,31} = 1.151$, $p = 0.292$; simulated fire x prey availability x neighbor roots: $F_{1,31} = 0.613$, $p = 0.440$).
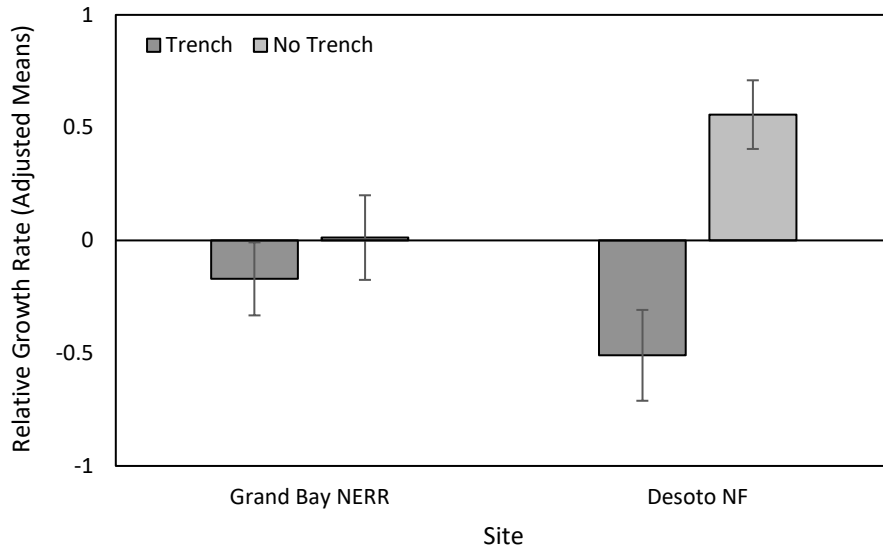
Figure 3: Change in relative growth rate (RGR) of target pitcher plants in response to site and trenching treatments between 2 and 17 months of the study. Error bars indicate ± standard error.
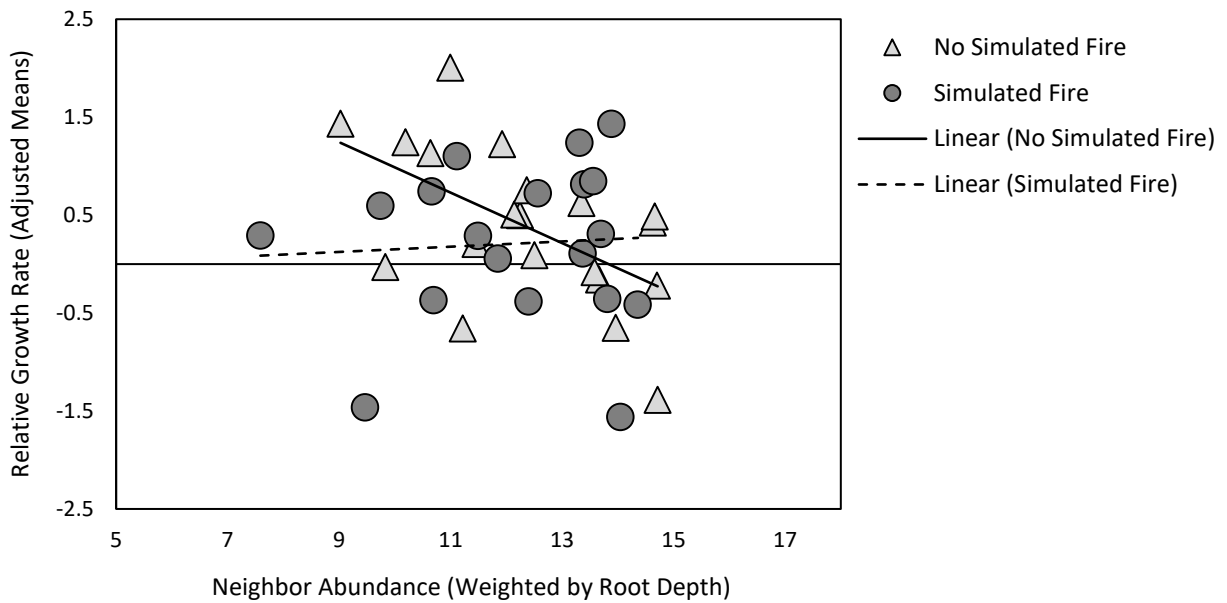
Figure 4: Relationship between relative growth rate (RGR) of target pitcher plants (treated with simulated fire and not treated with simulated fire) and abundance of neighbors weighted by root length in untrenched in plots.

Pitcher morphology responses to treatments

Pitcher plants may have responded to light-mediated increases in nutrient limitation following simulated fire and reduced access to prey by increasing investment in open pitchers. The change in the pitcher volume to petiole length ratio between 2 and 17 months of the study revealed a significant simulated fire x prey availability interaction ($F_{1,58} = 5.052$, $p = 0.029$), where the prey exclusion treatments affected the plants subjected to simulated fire, but did not affect the plants left intact. Among the simulated fire treated plants, the pitcher volume to petiole length ratios increased in starved plants but not in plants that were not starved (Figure 5).
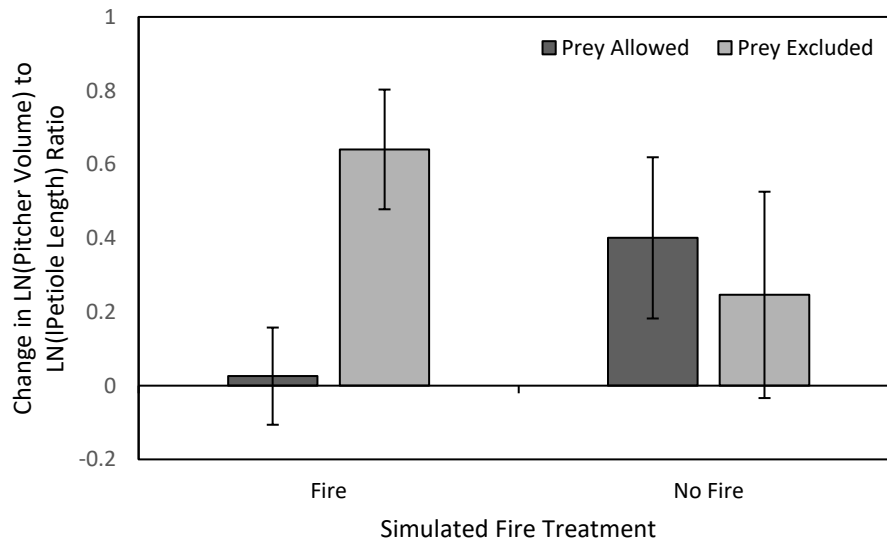
Figure 5: Change in pitcher volume to petiole length ratios of target pitcher plants in response to simulated fire and prey exclusion treatments between 2 and 17 months of the study. Error bars indicate ± standard error.

DISCUSSION

I found no support for any of the niche or disturbance-based hypotheses of species coexistence: Fire-mediated nutrient niche complementarity, fire-mediated competitive release, and nutrient-niche complementarity. In short, I found little evidence of competition in this study. I offer three non-mutually exclusive explanations for the observed lack of treatment effects in this experiment. I first discuss whether belowground competition and thus competition for nutrients is important in this system. I then discuss whether the lack of fire-mediated belowground competition was due to a lack of increased nutrient limitation. Finally, I consider whether I used an effective method for measuring belowground competition.

One possible reason why I saw little evidence of belowground competition in this system is that pitcher plants are simply not strongly affected by belowground competition from their neighbors under any of the circumstances examined here. Although, I observed a marginally significant negative correlation between pitcher plant RGR and the abundance of neighbors weighted by root length in the unclipped, the trenching treatments had neither a positive or negative effect on growth of pitcher plants at Grand Bay NERR, where accidental rhizome severing was minimal. Also, considering the marginally significant interaction between simulated fire and the abundance of neighbors weighted by root length in the untrenched plots, the clipping treatments had a negative effect on the pitcher plants where root competition was low, not where root competition was high. These results suggest that rather than affecting the plants by indirectly increasing or decreasing root competition from neighbors, clipping may have acted as an additional stressor to the plants in areas where abiotic conditions were already more stressful (and root competition was therefore lower). Two previous studies with *S. alata* found a significant effect of neighbor reduction on RGR (Brewer 1999b, 2003a), but the pitcher plants

themselves were not clipped, and competition in those studies was reduced using a sustained (press) reduction in both above- and belowground competition. Although I attempted to reduce belowground competition in a sustained fashion, there was no sustained reduction in aboveground competition in the current study. The fact that a sustained reduction in the belowground parts of neighbors alone had no positive effect on pitcher plant growth suggests that a sustained reduction in the aboveground parts of neighbors (including those of conspecifics) is necessary for competitive release. In their review of belowground competition in forests and woodlands, Coomes and Grubb (2000) found belowground competition generally to be more intense when light levels remained high for a period of time (as in large canopy gaps or forest edges). A sustained release from aboveground competition in this system may require intense disturbances that cause considerable mortality of neighbors of pitcher plants, as might be associated with locally high fire intensity in patches of high fuel loads (Brewer et al. 1996) or other, more intense, disturbances (Paniw et al. 2015). If so, then low-intensity fires may not reduce shade for a long enough period of time to reduce aboveground competition on established pitcher plants and thus may not be sufficient to substantially increase nutrient demand.

Another possible reason why I found no treatment effects on belowground competition is that my simulated fire treatment did not increase nutrient limitation of growth, as predicted. Because the fertilizer associated with my simulated fire treatment did not contain nitrogen, I predicted that the simulated fire treatment would increase nitrogen limitation. This prediction was based on the assumption that nitrogen limitation would increase if the availability of light and nutrients other than nitrogen increased, but nitrogen did not (or at least not as much as other limiting resources). I also predicted that prey exclusion would exacerbate nitrogen limitation of growth based on the assumption that prey were primarily a source of nitrogen for the pitcher

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plants. It is possible one or both of these assumptions was not correct. First, although I added no nitrogen, increased soil temperatures associated with my clipping treatment could have increased nitrogen mineralization rates and thus the availability of nitrogen in the soil to pitcher plants (Dean et al. 2015). If so, nitrogen limitation might not have increased in response to my simulated fire treatment. Second, prey provide a source of both nitrogen and phosphorus to pitcher plants (Christensen 1976; Ellison 2006). Hence, the increase in phosphorus from fertilizer addition might have reduced the necessity of prey for overcoming phosphorus limitation.

In the current study, pitcher plants may have avoided increases in nutrient limitation associated with simulated fire through phenotypic plasticity in carnivory investment. Pitcher plants responded to increased light following simulated fire combined with reduced access to prey when starved by subsequently increasing investment in open pitchers. The pitcher volume to petiole length ratio increased in starved plants subjected to simulated fire but not in plants that were subjected to simulated fire but not starved. These results suggest that my simulated fire treatment (increased light, P, K, and Mg) did increase prey-derived nitrogen limitation, at least temporarily. I therefore am not prepared to abandon the hypothesis that nitrogen becomes more limiting after fire and that carnivorous plants respond by allocating more resources into acquiring prey-derived nitrogen. I predict that redoing the experiment in this paper using the alternative method of reducing root competition described below would reveal a negative impact of root competition on individuals that have been exposed to reduced aboveground competition and have been denied access to prey. In other words, when the plants are denied nitrogen from prey after fire, they will be forced to compete for nitrogen belowground (supporting the FMNNC hypothesis).

A final reason why I saw no evidence of competition is that my method of reducing belowground competition (trenching), despite its widespread use (Coomes and Grubb 2000), might not have been effective in my system. Trenching not only prevents roots of neighbors from growing near those of the target plant, it also confines the roots of the target plant to a limited volume of soil. In addition, trenching potentially damages belowground parts of the target plants. Given the issues with the trenching treatments, I suggest that this same experiment be repeated but with a different means of testing belowground competition effects. All approaches have artifacts, but an alternative approach that might be more appropriate for my system would involve applying the pitcher starvation and fire simulation treatments described in this study, but replacing the trenching treatments with herbicide treatments (killing the neighbors outright, but leaving the focal pitcher plant intact). Artificial shade cloth could then be placed over all plots assigned to 'reduced root competition/aboveground competition-intact' treatments (Brewer 2003b). If the negative effect of starving pitchers is greater when comparing clipped to unclipped plots with intact neighbors (the simulated fire treatment) than when comparing unshaded to shaded plots with neighbors removed, then such a finding would indicate that a sustained reduction in aboveground competition increases belowground competition for nutrients between pitcher plants and their neighbors.

CHAPTER II: THE EFFECTS OF SIMULATED FIRE AND SOIL NUTRIENT ADDITION

ON CARNIVORY AND ARBUSCULAR MYCORRHIZAL INVESTMENT IN TRACY'S

THREADLEAF SUNDEW

ABSTRACT

The cost-benefit model for carnivory in plants posits that carnivory should only be beneficial when nutrients are limiting to growth; nevertheless, fire-adapted carnivorous plants appear to challenge this assumption by growing more abundant as both light and nutrients become more available after fire. One possible explanation for this apparent paradox is that the nutrients made more available after fire are not the same as those made available by prey. Since ash deposited after fire in nutrient-poor pine savannas primarily consists of phosphorus (P), potassium (K), and magnesium (Mg), I hypothesized that carnivorous plants rely on leaf traps for the acquisition of prey-derived nitrogen (N) as soil N becomes more limiting. I also hypothesized that arbuscular mycorrhizal fungi (AMF) help carnivorous plants to acquire P, K, and Mg when growth is no longer limited by N. Finally, I hypothesized that investment in both carnivory and AMF colonization is limited primarily by light during periods without fire. I tested these hypotheses in a field experiment by examining the effects of varying nutrient availability (N fertilizer vs. P, K, and Mg fertilizer) and light availability (vegetation clipping vs. no clipping) on carnivory (i.e., leaf mucilage production) and AMF colonization in Tracy's threadleaf sundew (*Drosera tracyi*). My results did not support any of my hypotheses. Instead, a marginally significant fertilizer treatment effect on mucilage production suggested that *D. tracyi* growth may be partially limited by P, K, and/or Mg. Also, despite observing AMF in the roots of *D. tracyi* in a pilot study performed in 2013, I did not find any AMF colonizing the plants used in the experiment performed in 2016. Since I only observed AMF colonization during the plant's flowering season in the year of the pilot study, I suggest that AMF colonization in *D. tracyi* is tied to phenology. Overall, this study suggests that late season fire may have little to no effect on

resource investment in a species of carnivorous plant that is relatively tall and therefore less

likely limited by light during periods without fire.

INTRODUCTION

Many carnivorous plants are associated with nutrient poor, fire-prone habitats and often increase in abundance and/or increase investment in carnivory (e.g., produce larger leaf traps) following fires (Brewer 1999a,b,c, 2001, 2003; Luken 2007; Kesler et al. 2008)). Such an association between carnivorous plants and fire has been described as a paradox, given that the availability of soil nutrients often increases following fire (Givnish 1989; Gillon et al. 1995). One possible explanation is that the nutrients made more available after fire are not the same as those made available by prey. Prey have been demonstrated to be especially important as a source of nitrogen (N) (Christensen 1976; Ellison 2006), whereas ash tends to add phosphorus (P), potassium (K), and magnesium (Mg) to the soil (Christensen 1993; Brewer, unpublished data). Taken together, these responses suggest that post-fire increases in carnivory are driven by N limitation. Otherwise, why would investment in carnivory increase at the same time the availability of other nutrients (e.g., P, K, and Mg) increases (Givnish et al. 1984)?

Investment in N-acquiring carnivorous traps may rise following fire to support increased investment in adaptations for acquiring P, such as arbuscular mycorrhizal fungi (AMF). Despite the longstanding assumption that an association between carnivorous plants and AMF would be redundant and therefore absent (Juniper et al. 1989; Adlassnig et al. 2005; Brundrett 2009), studies within the past decade have shown that several species within the carnivorous genus, *Drosera*, are mycorrhizal (Fuchs and Haselwandter 2004; Weishampel and Bedford 2006; Quilliam and Jones 2010; Harikumar 2013). However, the question remains: why be both carnivorous and mycorrhizal? I propose that like mycorrhizal legumes, where rhizobium contributes N and AMF contributes P to the plants (Jia et al. 2004), AMF may be important for enabling carnivorous plants to access nutrients in the soil that are not readily available from prey

after fire. In fact, in accordance with the trade balance model described by Johnson (2010), a positive feedback loop may occur between the carnivorous leaf traps and AMF colonized roots after fire if the plant contributes photosynthates to the AMF as a result of enhanced light and N capture via robust post-fire leaf traps, which in turn maximizes the uptake of temporarily available nutrients (e.g., P, K, and Mg) that are directly or indirectly beneficial for photosynthesis and leaf trap development for overcoming elevated competition for post-fire N.

Conversely, an alternative explanation for the apparent paradoxical association between carnivorous plants and fire may have nothing to do with changes in nutrient availability. While individual fires may result in short-term increases in ash-derived P, K, and Mg, and increased rates of mineralization following fire could even increase the availability of N (Dean et al. 2015), the net long-term effect of frequent fires in habitats with sandy, nutrient poor soils may actually be to reduce nutrient availability due to volatilization of organic N (Christensen 1993) and leaching of water-soluble ions (Lewis 1974). Increases in carnivorous plants following individual fires may simply reflect light-stimulated emergence from a seed or bud bank by species that are adapted to chronically infertile soils and fire or another disturbance (Brewer 1999a,b,c; Luken 2007). Such increases may therefore be completely unrelated to the small, ephemeral increases in nutrient availability associated with individual fires.

The goal of this study was to address three hypotheses: (1) mycorrhizal carnivorous plants depend on carnivory when growth is limited by the availability of N; (2) mycorrhizal carnivorous plants depend on AMF when growth is limited by the availability of P, K, and Mg; and (3) carnivory and AMF colonization in mycorrhizal carnivorous plants is primarily limited by light availability and only respond to changes in nutrient availability immediately after fire. I tested these hypotheses using mycorrhizal Tracy's threadleaf sundew plants (*Drosera tracyi*) in a

field experiment where I factorially manipulated two important aspects of fire: nutrient (P, K, and Mg vs. N) addition and aboveground vegetation removal.

METHODS

Location

This study was conducted in two separate pitcher plant bogs (hereafter, Sandy Creek and Wolf Branch) in Desoto National Forest in Stone County, Mississippi, USA. The bogs at both the Sandy Creek (30°73' N, -88°96' W) and Wolf Branch (30°73' N, -88°98' W) sites are open, hydric pine savannas possessing a sparse canopy dominated by *Pinus elliottii* and possessing a rich, mostly herbaceous understory dominated by *Ctenium aromaticum.* Both sites have been historically maintained by frequent fires (1-3 times a decade) and have been relatively unimpacted by severe anthropogenic disturbance.

Focal Species Selection

In June 2013, I conducted a pilot study to determine if any carnivorous plants at Desoto National Forest possessed roots colonized by AMF. Given that several published studies have shown AMF in *Drosera* around the world (Fuchs and Haselwandter 2004; Weishampel and Bedford 2006; Quilliam and Jones 2010; Harikumar 2013), I decided to collect roots from five individual specimens of *Drosera tracyi* at Sandy Creek. Also, despite the lack of published studies showing AMF in *Sarracenia*, recent unpublished work had suggested that *S. alata* may also associate with AMF (Harper et al., unpublished data). Therefore, I also collected roots from five specimens of both *S. alata* and *S. psittacina.* Once I collected the roots, I brought them back to the University of Mississippi for clearing and staining (see below for procedure). Of the

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collected specimens, I detected AMF in three out of the five *D. tracyi* individuals (Figure 6), within which I observed a mean colonization rate of 27.33% ± 4.38. Given that AMF was only detected in *D. tracyi,* I selected *D. tracyi* to be the focal species used in the following experiment.
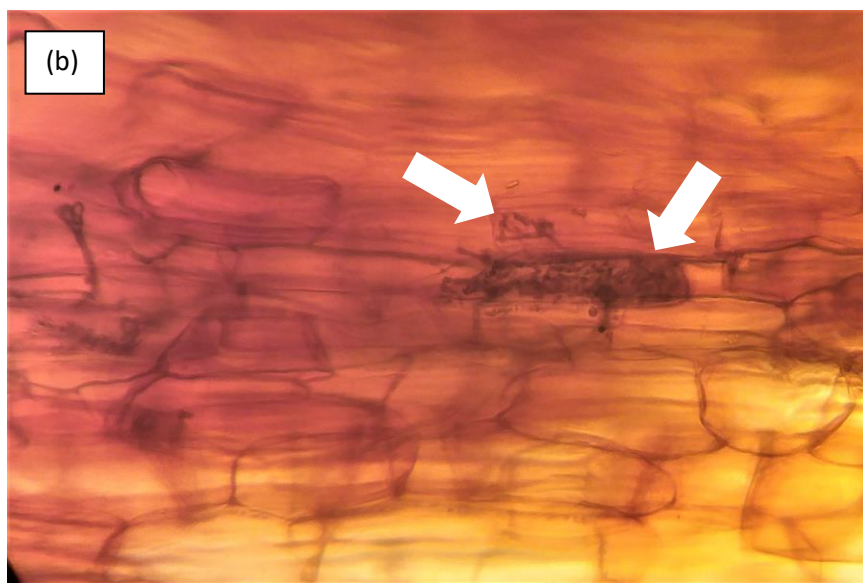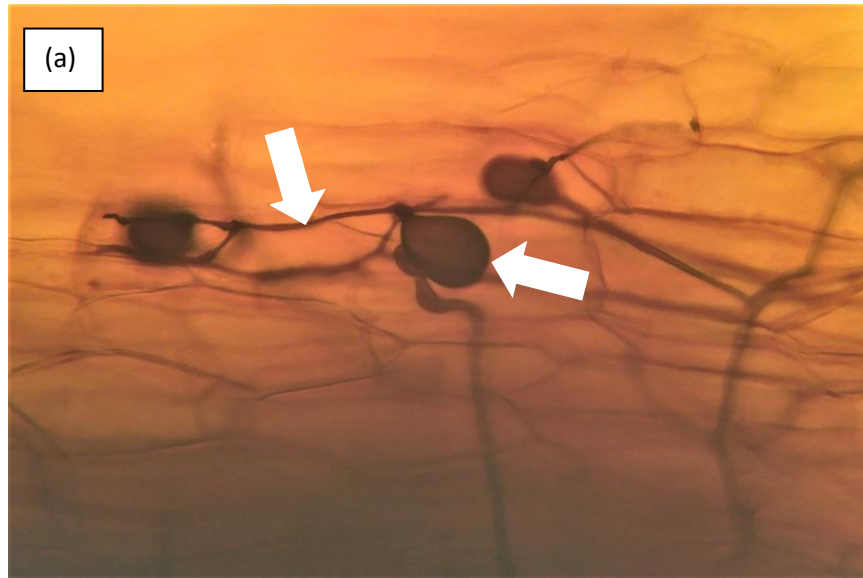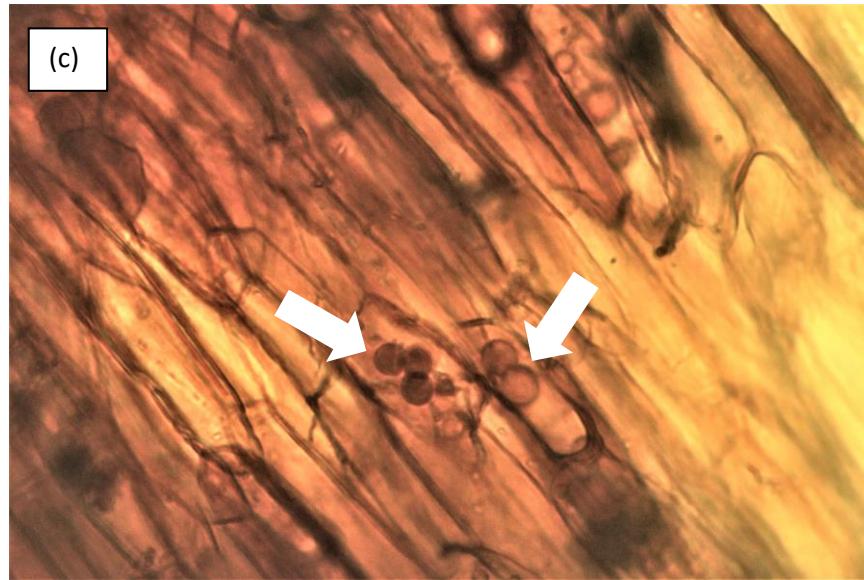
Figure 6: Microscopic visualization of (a) hyphae and vesicles, (b) arbuscules, and (c) spores in AMF-colonized roots of *Drosera tracyi*.

Experimental Setup

To mimic the effects of fire stimulated changes in soil nutrient availability and light availability on carnivory investment (mucilage production) vs. mycorrhizal investment in *D. tracyi*, I factorially manipulated aboveground vegetation removal and nutrient inputs that might be expected from ash deposition (e.g., P, K, Mg) or increased mineralization (e.g. N). In August 2016, I established 30 1 m^2 plots, each around an individual *D. tracyi*, within the pitcher plant bogs at Sandy Creek and Wolf Branch sites. I then randomly assigned half of the plots to vegetation clipping treatments and non-clipping treatments. Within each of these clipping/no clipping treatments, I randomly applied either fertilizer containing N (0.02 g/m^2) only, fertilizer containing P (0.02 g/m^2), K (0.015 g/m^2), and Mg (0.003 g/m^2) only, or no fertilizer to each plot. The plots that received no fertilizer were sprayed with equivalent amounts of water to control for

the watering effect of fertilizer addition. At each site, each treatment combination had a sample size of five.

Data Collection

Like other species in the *Drosera* genus, *D. tracyi* produces a sticky, polysaccharide-rich mucilage on the upper surface of its leaf tentacles for luring and capturing prey (Rost and Schauer 1977). Therefore, to quantify investment in carnivory in terms of mucilage production, I measured leaf stickiness (a proxy for mucilage production) of the longest leaf of each target plant before and three weeks after treatment application by measuring the force required to separate a 4 cm x 2 cm piece of folded filter paper from the leaf using a dynamometer (Pensola, Schindellegi, Switzerland). This measure of leaf stickiness allowed me to indirectly quantify mucilage production and/or the concentration of polysaccharides in the mucilage (Thoren et al. 2003). In addition to the target plant measurements, I also measured groundcover leaf area index (LAI) (a proxy for shade or aboveground competition) before treatments and percent soil moisture before and after treatments. Groundcover LAI was measured using a LI-COR plant canopy analyzer (LI-COR Biosciences, Lincoln, NE), and soil moisture was measured using an Aquaterr M-300 portable soil moisture meter (Aquaterr Instruments, Costa Mesa, CA). After completing all the post-treatment field measurements, I harvested the target *D. tracyi* plants and brought them back to the University of Mississippi so that I could assess AMF colonization in the roots. In the lab, I carefully collected subsamples of roots from each excavated plant and rinsed them in water. I then cleared the root samples in 10% (w/v) KOH solution, stained them with 0.075% (w/v) Chlorazol Black E solution (Brundrett, Piche, and Peterson 1984), and mounted them on slides with polyvinyl alcohol-lactic acid-glycerol (PVLG) mounting medium

(Koske and Tessier 1983). I quantified percent root length colonization of AMF under a compound microscope (400X magnification) using the magnified line-intersect method (McGonigle et al. 1990).

Data Analysis

I used a three-way ANCOVA (type III sums of squares) to analyze the effects of site (treated as a fixed effect), the clipping and fertilizer treatments, and their interactions on leaf stickiness and AMF colonization rates. I used a type II sums of squares method (a more powerful means for detecting significant main effects than type III sums of squares) for instances where I did not observe any significant treatment interactions. Initial LAI and average soil moisture were investigated as possible environmental covariables; however, simple regressions of the response variables corrected for site with the possible covariables revealed that neither was significant. I log-transformed all response data to better meet the ANOVA assumptions of normality and homoscedasticity. Finally, I performed retrospective power analyses if I found no significant main treatment effects to determine the adequacy of my sample size.

Predictions

A significant main effect of nutrient treatment such that the addition of N, but not P, K, and Mg, reduced leaf mucilage production supported the hypothesis that carnivory is most beneficial to *D. tracyi* when N is most limiting to growth. Second, a significant main effect of nutrient treatment such that the addition of P, K, and Mg, but not N, reduced root colonization by AMF supported the hypothesis that AMF are most beneficial to *D. tracyi* when P, K, and Mg are most limiting to growth. Third, a significant main effect of aboveground vegetation removal such

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that both investment in carnivory and AMF root colonization increased most when aboveground

vegetation was removed, irrespective of nutrient treatment, supported the hypothesis that

carnivory and AMF are most beneficial to growth when light does not limit growth (e.g.,

immediately after a fire).

RESULTS

Overall, my results did not support any of my hypotheses explaining the relative role of

light and nutrient type (i.e., prey-derived N vs. ash-derived P, K, and Mg) in regulating relative

investment in carnivory vs. AMF colonization in *D. tracyi*. Regarding the stickiness analyses, I

did not observe a significant treatment interaction using the type III sums of squares method

(Site x Clipping x Fertilizer: $F_{2,47} = 0.941$, $p = 0.397$); therefore, I did not see any signs that

increased light availability through clipping increased nutrient limitation or vice versa. I did

observe a marginally significant main effect of fertilizer when using the type II sums of squares

method, whereby leaf stickiness was slightly reduced after exposure to P, K, and Mg fertilizer

($F_{2,54} = 2.407$, $p = 0.099$; Figure 7). Leaf stickiness did not appear to increase or decrease in

response to the clipping treatments ($F_{1,54} = 1.087$, $p = 0.302$). A highly significant site effect

suggested that the plants produced more mucilage at the Sandy Creek site than at the Wolf

Branch site ($F_{1,54} = 7.949$, $p < 0.001$). Retrospective power analyses revealed a power value of

only 0.480 for the main effect of the clipping treatment and 0.530 for the main effect of the

fertilizer treatment. Both these values were well below the level of 0.8 which is often considered

adequate (e.g., Cohen 1988); therefore, I caution that the lack of significant treatment effects

may be due to low statistical power. Finally, although I found AMF colonizing *D. tracyi* roots in

the 2013 pilot study, I did not observe any signs of AMF colonization in any of the plants in the 2016 study.
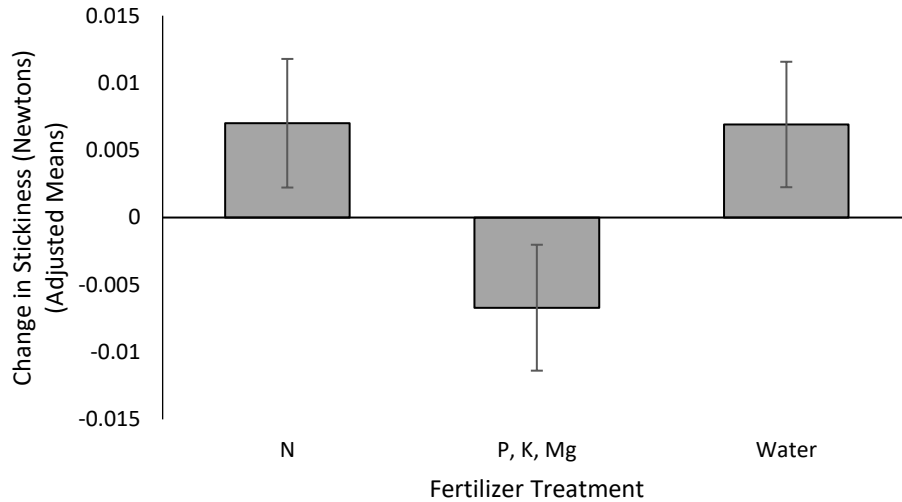
Figure 7: Effects of fertilizer treatment on Tracy's threadleaf sundew leaf stickiness. Error bars indicate ± standard error.

DISCUSSION

I found no evidence in support of my hypotheses explaining the relationship between resource availability and relative investment in carnivory vs. AMF colonization in carnivorous plants. The marginally significant decrease in leaf stickiness in response to the P, K, and Mg fertilization but not N fertilization contradicts my prediction that investment in carnivory would decrease when exposed to increased N but not P, K, and Mg. These results could mean one of two things: (1) *D. tracyi* depends on carnivory for the acquisition of P, K, and Mg, but not N; or (2) *D. tracyi* depends on carnivory for the acquisition of both P and N, (and possibly K and Mg), but increases in available N concentrations were shorter-lived compared to increases in the availability of P in the soil due to greater solubility of the nitrate component of the N fertilizer

compared to the phosphate component of the P, K, and Mg fertilizer. Consequently, the small

amount of N in the fertilizer treatment was not enough for the plants to overcome their N

limitation and decrease investment in carnivory, whereas the small amount of P added to the soil,

because of its greater persistence in the soil, was enough for the plants to overcome their P

limitation and decrease investment in carnivory. The first explanation is more in line with other

published accounts of carnivorous plants in higher latitude regions primarily taking up P from

prey (Chandler and Anderson 1976; Stewart and Nilsen 1993; Wakefield et al. 2005; Ellison

2006). However, it should be noted that the plants in these studies have likely shifted from N

limitation to P limitation in recent years due to increased atmospheric N deposition from

increased fossil fuel use in these regions (Wakefield et al. 2005). I suggest that future follow-up

studies incorporate leaf stoichiometric measurements to determine if *D. tracyi* is truly more

limited by P, K, and Mg than by N in Gulf Coastal pitcher plant bogs.

Despite the observed marginally significant fertilizer effect, the lack of a truly significant

clipping or fertilizer treatment effect contradicts the findings of Thoren et al. (2003), who

observed highly significant decreases in mucilage production in *D. rotundifolia,* in response to

increased shade and nutrient availability. Up to this point, all papers that have noted decreased

investment in carnivory in response to elevated nutrient exposure describe experiments where

plants were either exposed to a single high dose of fertilizer (Brewer 2003a), repeated doses of

fertilizer (Ellison and Gotelli 2002; Thoren et al. 2003), or the plants were transplanted into areas

with naturally high soil nutrient availability (Bott et al. 2008; Abbott and Brewer 2016). Unlike

these past experiments, my fertilizer treatments mimicked the nutrient concentrations that is

typically added from natural fire, and my results suggest that *D. tracyi* does not respond

dramatically to such slight changes in nutrient availability. Therefore, one perhaps should not

expect dramatic shifts in carnivory investment in response to fire-mediated increases in nutrient availability. An interesting follow-up study would be to determine if the slight changes in mucilage production after ash deposition is accompanied by any real changes in prey capture rates. If prey capture rates fail to vary with the slight changes in mucilage production, that would suggest that such low levels of nutrients from ash are not adequate to affect carnivory. Hence, the strong association of carnivorous plants in fire-prone savannas with nutrient-poor soils may not be paradoxical after all.

Considering the lack of a significant correlation between leaf stickiness and initial LAI and average moisture availability, the absence of a significant clipping effect was not particularly surprising. According to the cost-benefit model, carnivory should be most beneficial when photosynthesis is not limited by resources such as water and light (Givnish et al. 1984), and that is why many carnivorous plants are restricted to open, wet habitats (Zamora et al. 1998; Brewer et al. 2011). Considering the importance of light and moisture availability to the cost-benefit model, the lack of a correlation between leaf stickiness and LAI and average moisture suggests that neither light nor moisture were limiting factors at either field site, and thus any slight effects the clipping treatment might have had on light or moisture availability were inconsequential. *Drosera tracyi* is unique among the species of sundew of North America in that it produces long tentacle-like leaves that can grow up to 54 cm tall (Schnell 2002; Personal Obs.), and it is likely for this reason that the plant was less responsive than its much shorter-statured congenerics (e.g., *D. capillaris* (Brewer 1999a)) to aboveground vegetation removal. These results also suggest that the presence of phenotypic plasticity in carnivory investment in response to variation in light, nutrients, and/or water is not necessarily to be expected if the carnivorous species consistently occurs in sunny and wet habitats with nutrient-poor soils. Demonstrating a strong association

with such habitats may require experiments that involve transplanting the species to shadier and/or drier habitats or to those with nutrient-rich soils, where the species is naturally absent (e.g., Abbott and Brewer 2016).

To my knowledge, the pilot study described in this paper is the first published account of AMF in a species of carnivorous plant in the southeastern United States. This research also adds an additional member to the growing list of *Drosera* species within which AMF has been detected. Prior to this study, AMF colonization has been noted in *D. rotundifolia* in the northeastern United States (Weishampel and Bedford 2006) and in the United Kingdom (Quilliam and Jones 2010), in *D. burmanii* and *D. indica* in southwestern India (Harikumar 2013), and in *D. intermedia* in Austria (Fuchs and Haselwandter 2004). To date, colonization by AMF has yet to be described for any other genus of carnivorous plant in the literature.

Despite this study's contribution to the growing evidence that AMF exists in the carnivorous genus *Drosera*, my experiment failed to identify the reason behind this seemingly peculiar association. Nevertheless, my findings are consistent with other studies that have found irregular colonization by AMF in *Drosera* (Weishampel and Bedford 2006). The fact that the AMF were not detected in the roots of *D. tracyi* in August of the experimental year, but were present in the specimens sampled in June of the pilot study year, suggests that the AMF are more strongly tied to season. Such seasonal variation has been observed in other species of *Drosera* (Fuchs and Haselwandter 2004; Quilliam and Jones 2010)*,* and this pattern is similar to those observed in other non-carnivorous wetland species where AMF colonization rates were found to be more strongly influenced by phenology than by variation in abiotic factors (Stenlund and Charvat 1994; Carvhalo et al. 2001; Bohrer et al. 2004). The typical flowering season for *D. tracyi* is May through June (Schnell 2002), and it is possible that demand for P was higher during

this period, thus requiring AMF. Of course, I cannot discount any possible differences in underlying conditions between sampling years; therefore, I suggest that future studies further evaluate the potential role AMF may play in *Drosera* phenology across multiple full growing seasons. If it turns out that *Drosera*-associated AMF is typically ephemeral, any past discrepancies in the mycorrhizal status of carnivorous plants could be the result of sampling regimes where the plants were deemed 'non-mycorrhizal' because they were sampled during periods of no colonization (Bohrer et al. 2004).

CHAPTER III: COMPETITION DOES NOT EXPLAIN THE ABSENCE OF A CARNIVOROUS PITCHER PLANT FROM A NUTRIENT-RICH MARSH

Publication Citation:

ABSTRACT

Why is the carnivorous pitcher plant, *Sarracenia alata* Wood, largely absent from eutrophic habitats? Two hypotheses are addressed: (1) *Sarracenia alata* is competitively excluded by non-carnivorous plants where resource availability is high and (2) *S. alata* cannot tolerate stressful conditions unrelated to competition in a eutrophic wetland. I tested these hypotheses using a reciprocal transplant experiment to compare the performance of *Sarracenia alata* in eutrophic marsh and oligotrophic bog, crossed with soil source and neighbor removal treatments. Multiple environmental co-variables were also measured to identify factors responsible for transplant performance. Survivorship was 46.5% greater in the bog than in the marsh, and a significant proportion of the variation was explained by higher redox potential in the bog. Transplants were not negatively impacted by neighbors in either community. Results lead me to reject the competitive inferiority hypothesis and provide support for a hypothesis of inadequate stress avoidance. I suggest that a lack of tolerance of abiotic stressors, as opposed to competition, be given greater consideration when explaining the distributions of terrestrial hydrophytic carnivorous plants.

INTRODUCTION

Following his (1875) discovery that some plants gain nutrients from captured prey,

Charles Darwin hypothesized that the primary reason why some species are carnivorous is

because it allows the plants to thrive and maintain a competitive advantage in nutrient-poor soils.

The hypothesis that carnivory is an adaptation to nutrient-poor substrates gained general

acceptance (Ellison and Gotelli 2009), and, today, carnivory is generally seen as being analogous

to adaptations in non-carnivorous plants that supplement meager supplies of limiting nutrients in

the soil, such as nitrogen-fixing symbiotic relationships and mycorrhizae. Evidence in support of

the hypothesis that carnivorous plants are favored in nutrient-poor substrates comes primarily

from controlled studies that demonstrate plastic reductions in carnivory investment in favor of

increased investment in shade avoidance or reduced performance of terrestrial carnivorous plants

(e.g., Sarraceniaceae, Droseraceae) in response to increases in nutrient availability (Adamec

1997; Ellison and Gotelli 2002; Ellison 2006; Bott et al. 2008). In some cases, decreased

investment in carnivory with increasing substrate nutrient availability can be adaptive (Thorén

and Karlsson 1998; Zamora et al. 1998). In other cases, however, increased nutrient availability

can reduce both carnivory investment and the performance of some carnivorous plants (Ellison

and Gotelli 2002; Gotelli and Ellison 2002).

Although numerous studies have examined phenotypic plasticity in investment in

carnivory in response to nutrient availability, very few studies have tested whether carnivorous

plants are indeed at a competitive disadvantage in nutrient-rich substrates. A cost-benefit model

predicts that investment in carnivory puts carnivorous plants at a competitive disadvantage to

non-carnivorous plants in nutrient-rich wetlands because the benefit-to-cost ratio of producing

carnivorous traps declines with increasing substrate nutrient availability (Givnish et al. 1984).

Hence, by not producing carnivorous structures, non-carnivorous plants are free to invest more effort in light capture with increasing nutrient availability, thereby allowing them to outcompete carnivorous plants in nutrient-rich substrates (hereafter, I refer to this hypothesis as the competitive inferiority hypothesis). To test whether the competitive inferiority of carnivorous plants in nutrient-rich substrates is substantial enough to affect distributions of carnivorous and non-carnivorous species, one would need to show non-carnivorous plants adapted for nutrient-rich substrates competitively suppress or exclude carnivorous plants in nutrient-rich substrates. Wilson (1985) did conduct such a study with the carnivorous sundew, *Drosera intermedia*, but found that the sundew was only competitively suppressed by a non-carnivorous species in a relatively nutrient rich wetland when prey was excluded from its leaf traps. Also, the field site in which this transplant experiment took place was fully contained within the natural habitat of *D. intermedia* (Wilson 1985). I am aware of no published reciprocal transplant experiments demonstrating such competitive suppression occurring within eutrophic habitats where no carnivorous plants naturally occur.

An alternative hypothesis explaining the absence of some carnivorous plants from wet habitats with nutrient-rich soils is that such plants cannot tolerate abiotic stress that is positively correlated with nutrient availability (hereafter, the inadequacy of stress tolerance hypothesis). One example relates to the absence of wetland carnivorous plants from eutrophic wetlands (Brewer et al. 2011). Most carnivorous plants produce little or no aerenchyma (Seago et al. 2005; Adamec et al. 2006; Brewer et al. 2011). Although carnivorous plants may have alternative means of tolerating moderate hypoxia (Adamec 2005; Brewer et al. 2011), the production of roots with little to no aerenchyma may prevent many carnivorous plants from tolerating the severe hypoxia and associated stresses that are more likely to develop in nutrient-rich wetlands

than in nutrient-poor wetlands (Brewer et al. 2011). In contrast to the nutrient-poor wetlands where carnivorous plants are most likely to occur (e.g., pitcher plant bogs (Folkerts 1982)), nutrient-rich wetlands such as tidal marshes are often quite productive and tend to accumulate very organic soils (Odum et al. 1984) and approach complete anoxia. As a result, alternative chemical reduction and concomitant toxin accumulation tends to occur at a greater rate and throughout the soil profile in nutrient-rich wetlands than in nutrient-poor wetlands (Mitsch and Gosselink 2007). For instance, in acidic nutrient-rich wetlands where sulfate availability is high, the sulfate reduction pathway is often the dominant form of anaerobic bacterial respiration and the by-product, hydrogen sulfide, tends to accumulate and can be found in toxic concentrations even in the top 5-10 cm of soil (Lu et al. 2015). Tidal wetlands are especially susceptible to hydrogen sulfide accumulation since sulfates are regularly replenished by seawater. In fact, sulfate deposition has been shown to be just as important as exposure to the salt water itself in determining species composition in tidal wetland communities (Hackney and Avery 2015). In such nutrient-rich wetlands, the presence of well-developed root aerenchyma may therefore be necessary for aerating the rhizosphere and thus essential for plant survival (McKee et al. 1988; Ernst 1990; Luo et al. 2010). Hence, inadequacy of stress avoidance, rather than competitive suppression by non-carnivorous plants, may explain why few carnivorous plants in general are associated with nutrient-rich wetland soils.

In this study, I tested two hypotheses to explain the absence of a carnivorous pitcher plant from a nutrient-rich wetland within its natural range: competitive inferiority to non-carnivorous plants and inadequacy of stress avoidance. In order to test these hypotheses, I conducted a reciprocal transplant study where I examined the growth and survival of adult transplants of the carnivorous pale pitcher plant, *Sarracenia alata* (a species that possesses roots that are shallow

and that lack aerenchyma (Brewer et al. 2011), but still functionally absorbs nutrients to supplement nutrients obtained from prey (Adlassnig et al. 2005)). I examined growth and survival responses to variation in competition and soil source in a highly productive nutrient rich marsh exclusively occupied by non-carnivorous plants and in a less productive nutrient poor pitcher plant bog containing a high frequency and diversity of carnivorous plants. If competitive inferiority explained the absence of *S. alata* from a nutrient-rich marsh, I predicted that neighbor removal would have a much greater positive effect on growth and survival in the productive, nutrient-rich marsh than in the unproductive, nutrient-poor bog. If inadequacy of stress avoidance explained the absence of *S. alata* from a nutrient-rich marsh, I predicted that, despite the presence of productive non-carnivorous plants in the nutrient-rich marsh, *S. alata* would respond negatively to the harsh soil and/or drainage conditions associated with the marsh (compared to bog) and would be equally sensitive (or insensitive) to competition in the marsh and the bog.

METHODS

Study Site

This study was conducted in a pitcher plant bog within Grand Bay National Estuarine Research Reserve (30°27' N, 88°25' W) and in a tidal low-salinity (≤ 3 ppt) marsh along the Pascagoula River in the Sandhill Crane National Wildlife Refuge (30°26' N, 88°37' W). Both reserves are located within Jackson County, MS and, together, they contain some of the largest intact tracts of emergent marsh and bogs in the Gulf Coastal plain. Both sites have been relatively unimpacted by severe anthropogenic disturbance (MSCNWR 1996; Hilbert 2006). The pitcher plant bog possessed a sparse overstory of *Pinus elliottii*, but was densely covered with a

rich herbaceous understory dominated by *Aristida stricta*. The marsh possessed a fully open overstory, but was densely covered with an herbaceous community dominated by S*agittaria lancifolia* and *Cladium jamaicense*. *Sarracenia alata* Wood, which occurs naturally in pitcher bogs, reaches an average maximum height of 44 cm (pers. obs.), and its most frequent neighbor, *A. stricta*, reaches an average maximum height of approximately 48 cm (Outcalt et al. 1999). The vegetation in the marsh grows to be much taller, with *S. lancifolia* and *C. jamaicense* reaching average maximum heights of approximately 100 and 200 cm, respectively (Brewer and Grace 1990).

Preliminary observations revealed that hydrology differed between the tidal low-salinity marsh and the pitcher plant bog, with hydroperiods and flooding frequency being greater in the former. These differences undoubtedly could influence the growth and survival of *S. alata* transplants, irrespective of any habitat-related differences in soil fertility. I predicted, however, that poor drainage and high soil fertility could act synergistically to reduce soil oxidation-reduction potential. Hence, I predicted the greater negative effect of poorer drainage in the marsh compared to the bog would be exacerbated by the higher soil fertility of the marsh soil compared to the bog soil.

Experimental Setup

In order to evaluate pitcher plant competitive ability and the role habitat type and soil type plays in shaping pitcher plant dynamics, I factorially manipulated surrounding vegetation in two planting locations (hereafter, "site") as well as the source from which the potting soil was originally obtained (eight unique treatment combinations). I established forty 1 m² plots in a pitcher plant bog and a tidal low-salinity marsh in December 2013. At each site, 15.24 cm

diameter and 15.24 cm deep mesh pots containing marsh soil or pitcher plant bog soil were placed in pre-dug holes so that the top of the soil in the pots was level with the surrounding soils. Half of the plots within each soil treatment had surrounding vegetation removed within the entire 1 m^2 area and the other half was left intact. Vegetation removal plots were periodically weeded throughout the growing season to remove any regrowth. Upon establishment of the plots, *S. alata* was excavated from a nearby pitcher plant bog and a ramet was planted in each pot. Once established, each combination of the three treatments had ten replicates.

Data Collection

Prior to treatment application, the diameter and height (minus the length of the basal support tissue (hereafter, the "petiole")) of the tallest pitcher in each ramet was measured in order to calculate pitcher volume. At the end of the following growing season (November 2014), survivorship was noted, pitcher volumes were remeasured, and the plants were excavated so that total dried biomass could be weighed. To nondestructively estimate initial biomass, the final pitcher volumes were regressed against final total dried biomass, the parameters for the line of best fit were obtained, and the initial volumes were inserted into the equation so that initial biomass values for each plant could be calculated. Together, the final weights and estimated initial weights were used to calculate relative growth rates (Brewer 2003a). To calculate relative investment in carnivory vs. shade avoidance, pitcher volume was divided by the length of the petiole in the tallest pitcher of each plant. Higher pitcher volume to petiole length ratios indicated that the pitcher plants were investing relatively more into carnivory, while lower pitcher volume to petiole length ratios indicated that the plants were investing relatively less into carnivory and more into shade avoidance (Brewer 2003a). Differences in productivity between the two sites

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were also measured by collecting, drying, and weighing neighbor resprouts from the neighbor removal treated plots in early spring. The soils within the pots were measured for redox potential (mV), organic matter (%), moisture (%), salinity (ppt), and nutrient content. Redox potential was tested monthly in the field using an Orion ORP electrode and the other factors were quantified in the lab after the pots were excavated at the end of the experiment. Organic matter (%) was measured via loss on ignition, moisture (%) was measured via the gravimetric method, and salinity (ppt) was measured with a YSI model 30 salinity meter after producing 5:1 mixtures of deionized water and dry, sieved soil in separate Erlenmeyer flasks. Finally, a subsample of soils from each of three randomly chosen plots within each treatment combination was sent to the University of Georgia Soil, Plant, and Water Analysis Laboratory to be separately analyzed for total ammonium, nitrate, phosphorus, and potassium. All the measured nutrients were found to be positively correlated with percent soil organic matter (ammonium: $t = 7.24$, $p < 0.001$; nitrate: $t = 2.64$, $p = 0.015$; phosphorus: $t = 4.94$, $p < 0.001$; potassium: $t = 6.17$, $p < 0.001$ (Table 1)) and thus organic matter was used as a proxy for nutrient availability in all of the plots.

Table 1: Soil physiochemical properties of the potted soil within each treatment combination of site (marsh or bog), soil source (marsh or bog), and vegetation removal treatment (intact or removed). Means are ± standard error.

Soil Property	Marsh Site				Bog Site			
	Marsh Soil		Bog Soil		Marsh Soil		Bog Soil	
	Veg. Intact	Veg. Removed	Veg. Intact	Veg. Removed	Veg. Intact	Veg. Removed	Veg. Intact	Veg. Removed
Total NH_4^+ (mg/kg)[a]	44.10 ±11.91	53.31 ±2.65	9.68 ±0.35	9.53 ±0.71	25.77 ±2.21	167.50 ±97.99	6.43 ±2.01	6.36 ±1.58
Total NO_3^- (mg/kg)[a]	38.42 ±18.36	30.06 ±11.57	0.58 ±0.18	0.61 ±0.13	1.42 ±0.22	2.39 ±0.93	2.78 ±0.90	4.82 ±1.10
Total P (mg/kg)[a]	180.72 ±99.05	103.20 ±41.66	3.31 ±0.31	3.96 ±0.63	5.35 ±1.03	8.78 ±3.95	1.76 ±0.33	1.35 ±0.37
Total K (mg/kg)[a]	792.70 ±151.44	685.46 ±28.74	68.11 ±7.05	60.03 ±5.11	86.77 ±15.25	95.26 ±22.91	17.78 ±4.27	16.01 ±5.56
Organic Matter (%)	47.79 ±0.88	48.92 ±0.78	4.97 ±0.28	4.88 ±0.26	38.45 ±2.58	33.90 ±3.10	4.03 ±0.14	3.67 ±0.12
Moisture (%)	84.99 ±0.66	86.60 ±0.58	35.49 ±1.28	38.37 ±2.25	46.03 ±2.36	46.99 ±3.73	22.31 ±0.94	21.69 ±0.39
Salinity (ppt)	2.13 ±0.18	2.26 ±0.19	0.34 ±0.03	0.31 ±0.03	0.26 ±0.02	0.22 ±0.02	0.01 ±0.01	0.01 ±0.01
Redox Potential (mV)	-53.47 ±20.90	-95.53 ±25.50	-77.431 ±37.02	-96.20 ±24.51	131.20 ±19.79	116.78 ±19.69	174.68 ±9.45	166.44 ±14.03

[a] Nutrient analyses were performed on soils collected from a subsample of three randomly chosen plots within each treatment combination.

I acknowledge that the covariates included in the model were likely not an exhaustive representation of every important environmental factor (e.g., differences in prey composition, humidity, soil structure, specific soil toxin concentration, etc. may also be important). It is also likely that the factors that I did measure covary with other potentially important factors (e.g., redox potential likely covaries with sulfide, organic matter likely covaries with hydrology, etc.). My intent was not so much to identify each specific abiotic factor affecting the pitcher plants, though, but rather to measure the factors of likeliest importance in order to provide deeper insight into the site and/or soil treatment effects. Any follow-up studies looking to identify the specific abiotic factors affecting pitcher plant performance will likely need to involve more exhaustive surveys and experimental manipulation of the factors of interest.

Data Analysis

Initial comparisons of the measured environmental variables between sites were achieved by performing separate t-tests. Logistic regression was used to analyze both the main effects and interacting effects of the treatments (i.e., site x soil type x vegetation removal) on survivorship. Relative growth rates (RGR) and investment in carnivory vs. shade avoidance (pitcher volume to petiole length ratios) of surviving *S. alata* transplants were analyzed using three-way ANCOVA (type III sums of squares method), with initial biomass (Brewer 2003a) included as a covariate in the RGR analyses and the ratio data log-transformed to better meet the assumption of homoscedasticity. If no significant treatments interactions were observed, the type II sums of squares method (a more powerful means of detecting significant main effects than type III sums of squares) was used. The logistic regression and ANCOVA analyses were performed with and without the measured environmental covariates to determine which environmental differences

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between the two sites (habitat types) best accounted for differences in survivorship and growth of *S. alata* transplants. The Wald test was used to evaluate the significance of each covariate in the logistic regression model and the F-test of significance was used to evaluate the significance of each covariate in the ANCOVA model.

It should be noted that "site" was considered a fixed effect and one of the three treatment types; it consisted of two levels (marsh and bog). The random plot error nested within site, neighbor removal, and soil type was therefore used to test all main effects and interactions assuming a three-way factorial design. I acknowledge that there was no true replication of "site." My approach to dealing with the lack of (or pseudo-) replication of "site" was to use analysis of covariance to determine which measured environmental covariates were most important in accounting for the site differences in survival and growth. When either soil redox potential or organic matter were added to the model, I found that the significant effect of site disappeared. This result indicated to me that there were likely no differences between the two sites that affected survival or growth that were unrelated to (or uncorrelated with) soil redox potential or organic matter. In effect, I turned the pseudoreplicated effect of site into a regression analysis of multiple environmental variables that differed between the sites and that potentially could have affected survival and/or growth of the transplants.

Relationship between Statistical Results and Hypotheses

The two hypotheses tested in this study (i.e. competitive inferiority or inadequacy of stress avoidance) are alternative (but not necessarily mutually exclusive) hypotheses for the limitations imposed by carnivory in wet, nutrient-rich substrates. The competitive inferiority hypothesis was tested by examining the interaction between site and neighbor removal. An

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interaction indicating that *S. alata* were less capable of competing with the more productive marsh vegetation than with the less productive bog vegetation would be consistent with the hypothesis that the low benefit-to-cost ratio of being carnivorous in a productive habitat with a nutrient-rich soil puts *S. alata* at a greater competitive disadvantage in such a habitat. The competitive inferiority hypothesis does not predict that performance of *S. alata* will be worse in nutrient-rich marshes in the absence of competition. However, any additional benefit of growing in nutrient-rich soils will be too small to permit *S. alata* to effectively compete with non-carnivorous plants. Hence, the competitive inferiority hypothesis does not predict that there will be significant main effects of site or soil type. The inadequacy of stress avoidance hypothesis was examined through a series of tests. A significant main effect of site, such that *S. alata* performed worse in the marsh than in the pitcher plant bog (irrespective of neighbor treatment) would indicate that abiotic differences (e.g., soil drainage/anoxia differences) between the marsh and the bog were important in limiting the success of *S. alata* in marshes. A significant main effect of soil type such that *S. alata* did more poorly in the more fertile marsh soils, irrespective of neighbors, would indicate more chemically reduced conditions and/or nutrient or ion toxicity. A significant two-way interaction between site and soil type in which the poor performance of *S. alata* in nutrient-rich marsh soil was exacerbated by growing in the marsh would indicate that poorer drainage and higher soil fertility in the marsh act synergistically to reduce the survival and growth of *S. alata* transplants. If the effects of site and/or soil type were attributable to differences in soil anoxia-associated stress, then ANCOVA including soil redox potential should reveal a significant effect of soil redox potential that diminished the effects of sites, soil type, and/or their interaction on *S. alata* performance.

RESULTS

The marsh and the pitcher plant bog greatly differed in multiple aspects. First, percent

soil organic matter was significantly higher in the marsh than in the bog ($t = 48.97$, $p < 0.001$;

Table 1), and thus I assumed that nutrient availability was also higher in the experimental plots

in the marsh than in those in the bog. Similarly, soil moisture was higher in the marsh ($t = 54.71$,

$p < 0.001$; Table 1), salinity was higher in the marsh ($t = 11.83$, $p < 0.001$; Table 1), and

aboveground plant productivity was higher in the marsh ($t = 6.66$, $p < 0.001$). Likely as a result

of one or more of these aforementioned factors, redox potential was significantly lower in the

marsh than in the bog ($t = -14.23$, $p < 0.001$; Table 1).

With respect to survival, results provided no support for the competitive inferiority

hypothesis. The neighbor by site interaction was not significant ($z = -1.048$, $p = 0.295$). Although

neighbor removal interacted with soil type to influence survival ($z = -2.891$, $p = 0.004$; Figure

8a), the presence of neighbors increased the survival of *S. alata* rooted in marsh soil, while the

opposite was true for *S. alata* rooted in bog soil (Figure 8a).

Survival responses to the treatments provided partial support for the inadequacy of stress

avoidance hypothesis. Without any of the environmental covariates included, logistic regression

revealed a significant main effect of site, with survivorship being significantly higher in the bog

than in the marsh ($z = 1.985$, $p = 0.047$; Figure 8b). The site by soil type interaction was not

significant, though ($z = 0.008$, $p = 0.994$), suggesting that survivorship in the marsh was not

dependent upon the type of soil the transplants were planted in. Despite there being numerous

environmental differences between sites, only a couple of the covariates turned out to be

important in explaining site differences in *S. alata* survivorship. Re-running the analysis with

each of the covariates one at a time revealed that neither moisture ($z = 0.994$, p = 0.320) nor

salinity ($z = -0.972$, $p = 0.331$) had significant influences on survivorship. In contrast, a significant effect of redox potential ($z = 2.266$, $p = 0.024$) revealed that the probability of survival increased with increasing redox potential (Figure 9). A significant effect of organic matter (%) ($z = -2.027$, $p = 0.043$) further revealed that the probability of survival decreased with increasing organic matter (%) (Figure 10). Including redox potential and organic matter as covariates in the logistic regression model negated the effects of site, indicating that the significant effect of site on survivorship in the absence of covariate was largely related to site differences in redox potential and organic matter.
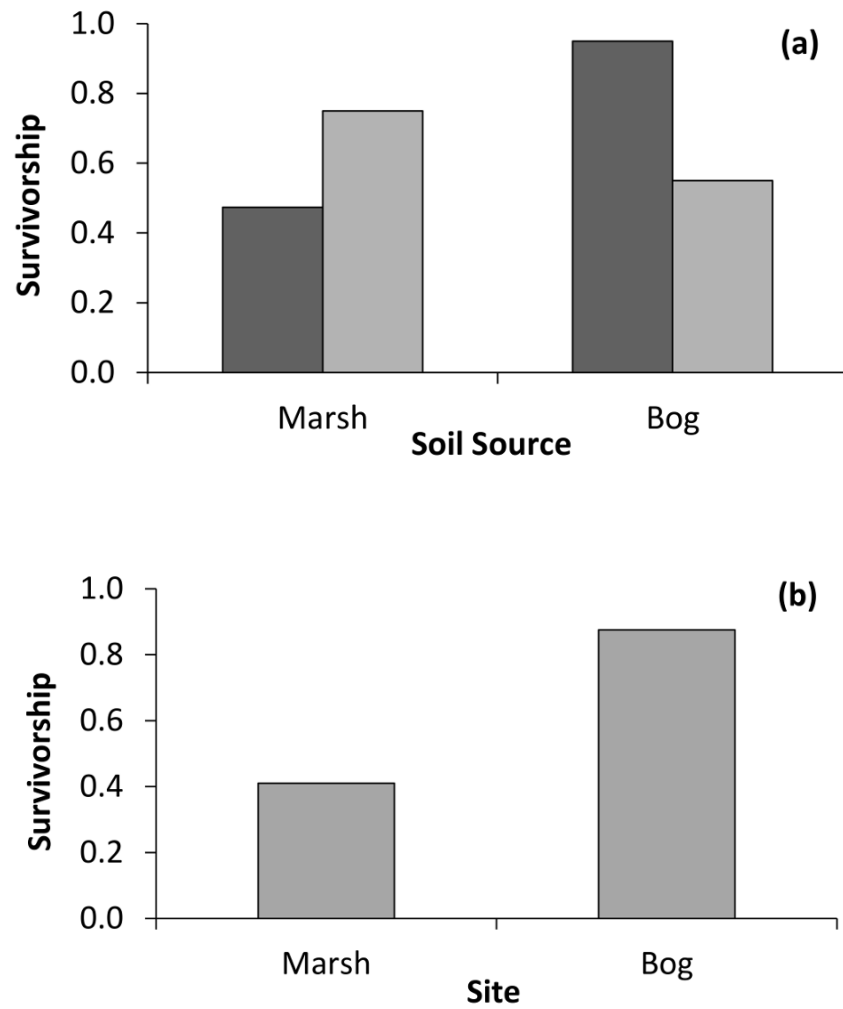
Figure 8: Survivorship of pitcher plant transplants in response to (a) neighbor removal and soil source (dark bars represent plots with neighbors removed and light bars represent plots with neighbors intact; $z = -2.891$, $p = 0.004$) and (b) to being transplanted into marsh or bog ($z = 1.985$, $p = 0.047$).
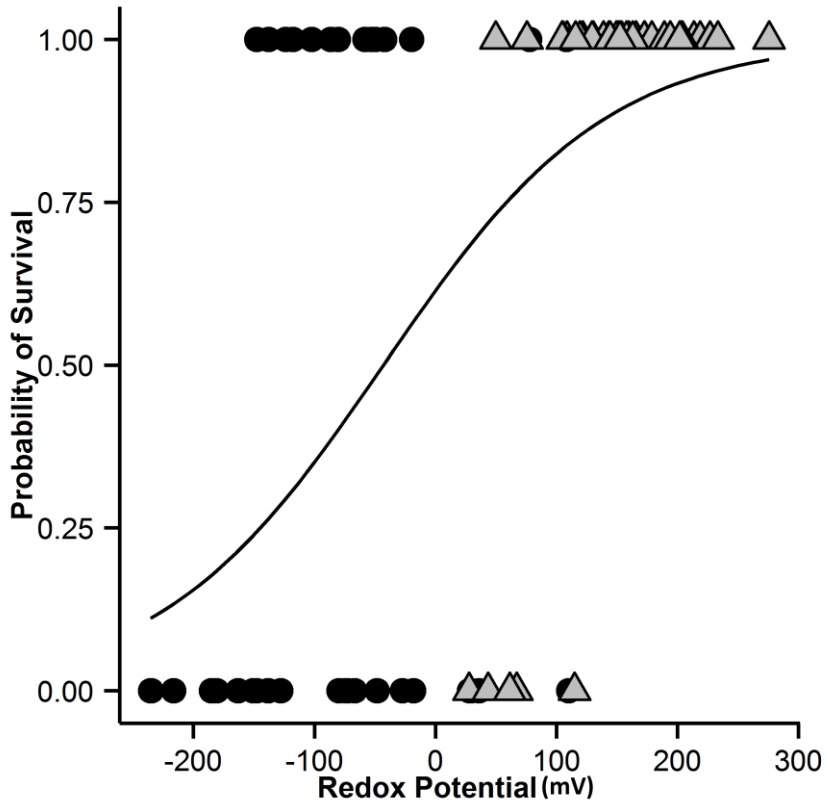
Figure 9: Logistic curve illustrating the relationship between redox potential (mV) and the probability of pitcher plant survival. The symbols correspond to the observed nominal response (Alive or Dead). Grey triangles represent plants in the bog site and the black circles represent plants in the marsh site. The y-axis applies only to the predicted logistic curve.
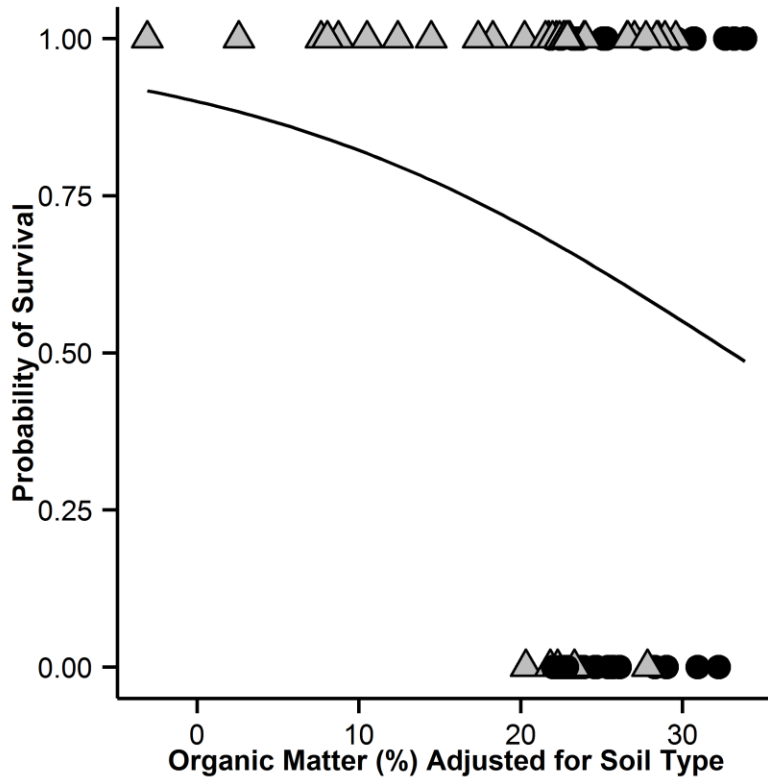
Figure 10: Logistic curve illustrating the relationship between soil organic matter (%) and the probability of pitcher plant survival. The symbols correspond to the observed nominal response (Alive or Dead). Grey triangles represent plants in the bog site and the black circles represent plants in the marsh site. The y-axis applies only to the predicted logistic curve.

Among surviving *S. alata* transplants, the RGR results further confirmed that competition for light was not more intense in the productive marsh than in the less productive bog. The interaction between site and neighbor removal was not statistically significant ($F = 0.047$, $p = 0.830$). Similarly, the responses of pitcher morphology showed no evidence that the pitcher plants were investing more in shade avoidance in response to the presence of the more productive vegetation in the marsh. Specifically, pitcher volume to petiole length ratios did not increase in response to neighbor reduction in the marsh. In fact, while the site by neighbor removal interaction was significant ($F = 4.508$, $p = 0.039$), transplants produced pitchers with

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higher volume to petiole length ratios in response to neighbor reduction in the bog, but not in the marsh.

In support of the inadequacy of stress avoidance hypothesis, RGR results indicated that pitcher plants were more stressed in the marsh than in the bog. Though no significant site by soil type interaction was observed using the type III sums of squares method ($F = 0.067$, $p = 0.798$), the type II sums of squares method revealed that the average RGR of survivors was lower in the marsh than in the bog ($F = 4.502$, $p = 0.039$ (no environmental covariates included); Figure 11). None of the environmental covariates were significant, however, when included in the model. It should be noted that although RGR was much lower for the plants in the marsh, RGR was also negative in the bog (Figure 11). The negative RGRs mean that the transplants most likely decreased in size and is probably reflective of an initial positive carry-over effect of clonal integration (rhizomes were severed in order to obtain transplants). Nevertheless, there was no treatment by initial size interaction, so I am not too concerned by the negative RGRs in the bog.
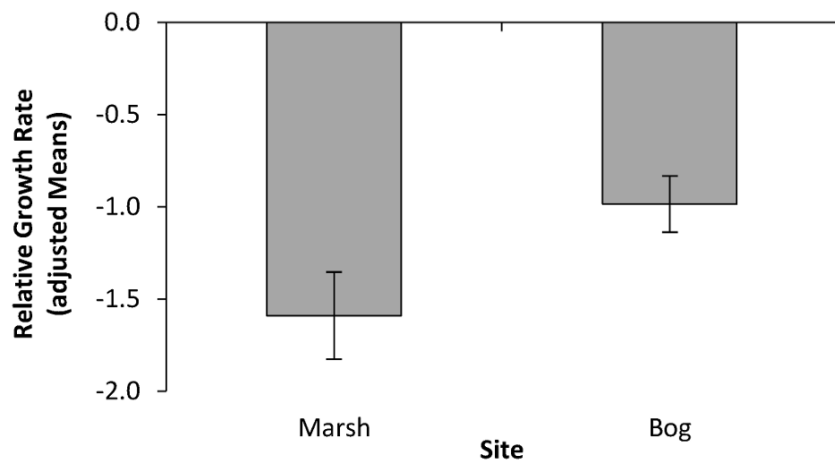

Figure 11: Effects of site on pitcher plant relative growth rate (RGR). Error bars indicate ±1 standard error.

In a manner consistent with there being greater soil nutrient availability in the marsh, the *S. alata* transplants overall produced pitchers with lower volume to petiole length ratios in the marsh than in the bog ($F = 12.254$, $p = 0.001$; Figure 12). However, there was no significant difference in pitcher morphology between soil types ($F = 0.472$, $p = 0.496$).
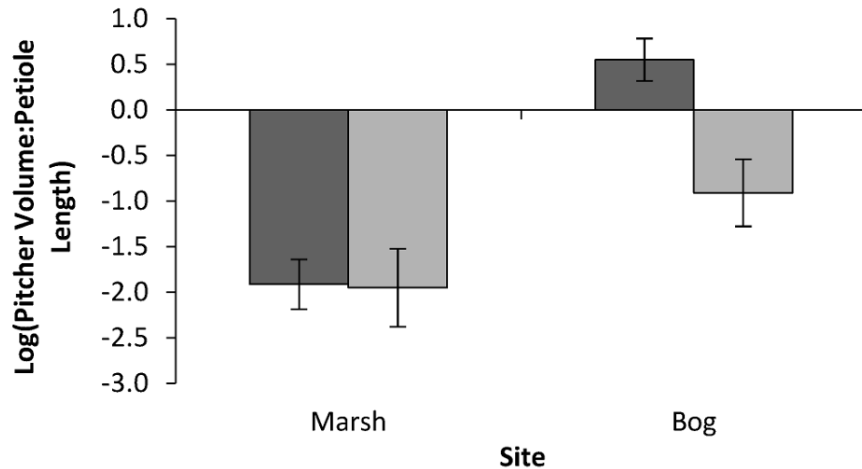
Figure 12: Effects of neighbor removal and site on Log(pitcher volume : petiole length). Dark bars represent plots with neighbors removed and light bars represent plots with neighbors intact. Error bars indicate ±1 standard error.

DISCUSSION

To my knowledge, this is the first study to experimentally examine how survival, growth, and carnivorous effort responded to both soil nutrient availability and competition from non-carnivorous plants in the field at sites with and without carnivorous plants. With this reciprocal transplant experiment I was able to show that competition was not the primary reason why a carnivorous pitcher plant was absent from a nutrient-rich marsh, and I also found evidence indicating that the pitcher plants were intolerant of the abiotic conditions in the marsh (e.g., extreme substrate hypoxia). These results therefore refute the competition inferiority hypothesis

and provide support for the inadequacy of stress avoidance hypothesis. The results provide a counterexample to the general claim that competition for light increases with increased soil fertility (Grime 1979; Twolan-Strutt and Keddy 1996). According to Grime's "competitors, stress-tolerators, or ruderals" (C-S-R) strategy hypothesis, long-lived, faster growing plants (i.e., strong competitors) should displace long-lived, slower growing plants (i.e. stress tolerators) from habitats where disturbance rates are low and soil resource availability is high (Grime 1979). However, *S. alata*—which most resembles Grime's definition of a "stress tolerator" (Brewer 1999b; Ellison et al. 2003)—was unaffected by the presence of neighbors in the more productive marsh. Instead, lower survival of *S. alata* with lower redox potential and higher organic matter indicates that this species was primarily intolerant of the stressors that accumulate in the highly-reduced marsh soils, whereas its predicted weak competitive ability was not apparent. Results of my study parallel those of transplant experiments in salt marshes, which found that intolerance of anoxic conditions, rather than competition, prevented species that dominated higher portions of the marsh (where nutrient supplies were lower but soil aeration was greater) from surviving well in the low marsh (where nutrient supplies were higher but soil aeration is lower) (Bertness 1991; Brewer 2003b; Pennings 2004). This study thus highlights an important limitation of applying general plant strategy theories to wetland ecosystems, in which multiple covarying stressors may be operating (Crawford 1992).

Interestingly, survivorship of the *S. alata* was lower in the nutrient rich marsh soil when neighbors were absent, suggesting that the neighboring plants had a facilitative effect (e.g., as seen in Bertness 1991). The *S. alata* transplants could have benefited from increased redox potential associated with increased shade from neighbors. However, the lack of a significant neighbor by redox interaction ($z = 0.89$, $p = 0.37$) or a significant neighbor by organic matter

interaction ($z = 0.59$, $p = 0.55$) suggests that the neighbors did not significantly increase redox potential or reduce nutrient levels within the marsh soils. Further research is needed in order to determine the cause of this apparent facilitation.

In contrast to the findings of Brewer (1999, 2003a), which found negative effects of neighbors on growth rate of pitcher plants in bogs, I found no negative effect of neighbors on growth rate or survival in the bog. One difference between the current study and those studies was the timing of the transplanting and implementation of the treatments. In the current study, transplanting and treatment applications were initiated at the end of the growing season, and then I harvested the transplants at the end of the following growing season. In Brewer (1999; 2003a), transplanting and/or monitoring and treatment application was initiated one month after the beginning of the growing season, and Brewer harvested plants one month after the beginning of the following growing season. Hence, the studies by Brewer examined the effects of treatments in one growing season (and part of the following growing season) on growth and survival in the following growing season, whereas I examined treatment effects throughout a single growing season. It is therefore possible that I underestimated the effects of competition on growth rate at both sites. Nevertheless, the dramatically reduced survival of transplants in the first growing season in the marsh rendered moot any delayed effects competition might have had on these transplants. Furthermore, Brewer (1999, 2003a) found no effects of neighbors on survival in the bog, and a lack of initial survival is likely the best explanation for why pitcher plants are absent from marshes.

The lack of evidence of a shade avoidance response of *S. alata* transplants to the presence of neighbors in the marsh was further evidence of the lack of importance of competition as a limiting factor in the marsh. The morphology of pitchers produced by *Sarracenia* has previously

been shown to vary profoundly with the availability of light and the presence of neighbors in bogs, and this phenotypic plasticity is believed to be an effective strategy for avoiding competition with non-carnivorous plants in bogs as these resources fluctuate (Brewer 1999b). Pitcher plants, for instance, appear to avoid competition for nutrients at the root level by investing in aboveground carnivorous structures when nutrients are limiting and they produce taller, flatter leaves (i.e., lower pitcher volume to petiole ratios) to maximize photosynthetic surface area when light is limiting (Ellison et al. 2003). Since pitcher plants exhibit phenotypic plastic responses to shifts in resource limitation in ecological time, the immediate effects of varying light and nutrient availability can easily be measured (Ellison and Gotelli 2002). Consistent with the cost-benefit model for botanical carnivory (Givnish et al. 1984), in the current study (as in Brewer 1999b, 2003a), the pitcher plants at the bog site minimized investment in carnivorous traps where photosynthesis was limited by light. In contrast, at the marsh site, *S. alata* showed no evidence of increased carnivorous effort at the expense of light capture in response to the removal of neighbors in the marsh. Irrespective of the presence of neighbors, the *S. alata* transplants appeared to function less as carnivorous plants in the nutrient-rich marsh than in the nutrient-poor bog. In the current study, *S. alata* produced greener and flatter pitchers with relatively low volume for prey capture in the marsh, with and without neighbors. Such a response is similar to that observed in experimental plots in the nutrient-poor bog to which N fertilizer was added (Brewer 2003a) and is consistent with numerous observations of reduced carnivorous effort in response to increased substrate nutrient supply (Adamec 1997; Ellison 2006; Ellison and Gotelli 2009). Such phenotypic plasticity is often viewed as evidence in support of the hypothesis that carnivorous plants are favored in nutrient-poor substrates and are at a competitive disadvantage in nutrient-rich substrates. Nevertheless,

the fact that I found no support for competitive suppression of *S. alata* by non-carnivorous plants in a nutrient-rich marsh illustrates the fact that studies of phenotypic plasticity in carnivory investment do not directly address the question of whether carnivorous plants are at a competitive disadvantage to non-carnivorous plants in substrates with high nutrient availability. In fact, phenotypically plastic reduction in carnivory investment in response to increased substrate nutrient availability could be a mechanism by which carnivorous plants are able to effectively compete with other plants as substrate nutrient supplies increase, provided that carnivorous plants are able to tolerate other stressors in habitats with nutrient-rich soils.

The current study provides support for the hypothesis that inadequate tolerance of hypoxia-associated stress could be one of several factors explaining the absence of carnivorous plants from some wetland habitats with nutrient-rich soils such as marshes with acidic but highly reduced soils. I do not mean to suggest that competition never prevents carnivorous plants from persisting in habitats with nutrient-rich soils. Rather, I argue that one should not assume that competition with non-carnivorous plants is the primary reason why carnivorous plants are absent from such habitats. A plastic reduction in carnivorous effort in nutrient-rich soils is not equivalent to reduced competitive ability of carnivorous plants in nutrient-rich soils. I therefore suggest that understanding what determines the habitat distributions of carnivorous plant species requires a different explanation from understanding what environmental factors favor increased or decreased investment in carnivory by a carnivorous plant within a given habitat. Given the complexity of multiple covarying biotic and abiotic factors along gradients of nutrient availability, if one is interested in determining whether carnivorous plants are at competitive disadvantage to non-carnivorous plants in nutrient-rich soil, I argue that there is no effective substitute for a competition experiment.

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VITA

EDUCATION

M.S., Plant Biology, Southern Illinois University, Carbondale
Thesis: "Effects of experimental storm surge and sedimentation on pitcher plants (*Sarracenia purpurea*) and associated assemblages in a coastal pine savanna"
Advisor: Dr. Loretta L. Battaglia
2012

B.S., Biology, Marian University, Indianapolis, IN
2010

PUBLICATIONS

Abbott, M.J. and J.S. Brewer. 2016. Competition does not explain the absence of a carnivorous pitcher plant from a nutrient-rich marsh. Plant and Soil 409:495-504.

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GRANTS AND AWARDS

2016 – NSF International Research Experience for Students (IRES) ($4763)
2015 – The Wetlands Foundation Conference Travel Grant ($1200)
2015 – Garden Club of America Award in Coastal Wetland Studies ($5000)
2014 – Sigma Xi Grant-in-Aid ($700)
2014 – Society of Wetland Scientists Grant-in-Aid ($1000)
2013 – University of Mississippi Graduate Student Council Research Grant ($1000)
2010 – Who's Who among Students in America's Universities and Colleges Award
2009 – Thoreau Award for Excellence in Writing in the Sciences, Marian University
2008 – Central Indiana Technical and Environmental Societies Award

PRESENTATIONS AND POSTERS

Poster Presentation: *Beaver-dredged canal function and development.* Annual meeting of the Association of Southeastern Biologists. Asheville, NC. 2010.

Poster Presentation: *Effects of experimental storm surge and sedimentation on pitcher plants and associated assemblages in a coastal pine savanna.* Midwest Ecology and Evolution Conference. Carbondale, IL. 2011.

Poster Presentation: *Effects of experimental storm surge and sedimentation on pitcher plants and associated assemblages in a coastal pine savanna.* Annual meeting of the Ecological Society of America. Austin, TX. 2011.

Oral Presentation: *Effects of experimental storm surge and sedimentation on pitcher plants and associated assemblages in a coastal pine savanna.* Annual meeting of the Ecological Society of America. Portland, OR. 2012.

Poster Presentation: *A new explanation for the rarity of carnivorous plants in habitats with nutrient-rich substrates.* Grand Bay NERR Research Symposium. Moss Point, MS. 2013.

Poster Presentation: *A new explanation for the rarity of carnivorous plants in habitats with nutrient-rich substrates.* University of Mississippi Graduate Student Council Research Forum. Oxford, MS. 2014.

Poster Presentation: *A new explanation for the rarity of carnivorous plants in habitats with nutrient-rich substrates.* Annual meeting of the Ecological Society of America. Sacramento, CA. 2014.

Oral Presentation: *Why don't carnivorous pitcher plants occur in nutrient-rich soils? The relative importance of competition and hypoxia intolerance*. Society of Wetland Scientists Annual Meeting. Providence, RI. 2015.

Oral Presentation: *Why don't carnivorous pitcher plants occur in nutrient-rich soils? The relative importance of competition and hypoxia intolerance*. Annual meeting of the Ecological Society of America. Baltimore, MD. 2015.

Oral Presentation: *Why don't carnivorous plants occur in nutrient-rich soils?*
University of Mississippi Three Minute Thesis Competition. Oxford, MS. 2015.

Poster Presentation: *Study of species interactions in the primeval forest of Białowieża, Poland*. University of Mississippi School of Pharmacy Annual Poster Session. Oxford, MS. 2016.