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Nutrient Availability Affects Flowering Rate but has Limited Influence on Morphology of the Hooded Pitcher Plant, Sarracenia minor.

Justin M. Lemmons
University of North Florida, j.lemmons@unf.edu

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NUTRIENT AVAILABILITY AFFECTS FLOWERING RATE BUT HAS LIMITED INFLUENCE ON MORPHOLOGY OF THE HOODED PITCHER PLANT, *SARRACENIA MINOR*

By

Justin Marc Lemmons

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CERTIFICATE OF APPROVAL

The thesis “Nutrient Availability Affects Flowering Rate but has Limited Influence on Morphology of the Hooded Pitcher Plant, *Sarracenia minor*” submitted by Justin Marc Lemmons.

Approved by the thesis committee: Date

_______________________________ ____________________
Anthony M. Rossi, Ph.D.
Committee Chair Person

________________________________ _____________________
Daniel C. Moon, Ph.D.

________________________________ ______________________
Dale A. Casamatta, Ph.D.

Accepted for the Department:

_________________________________ ________________________
Daniel C. Moon, Ph.D.
Chairperson

Accepted for the College:

__________________________________ _________________________
Barbara A. Hetrick, Ph.D.
Dean

Accepted for the University:

_____________________________________ __________________________
Len Roberson
Dean of the Graduate School

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ABSTRACT

Carnivorous plants perform as both producers and consumers. Botanical carnivory has evolved in sunny, moist, nutrient-poor environments, and the primary nutrient supplied by prey is proposed to be nitrogen. There is a trade-off between carnivorous and photosynthetic structures which corresponds to degree of carnivory expression and available nutrients. This study was conducted on the hooded pitcher plant, *Sarracenia minor*, which is a facultative wetland plant and Florida-threatened species. *Sarracenia minor* is considered a specialist myrmecophage and ants characterize the majority of attracted and captured prey. Ants not only provide nutritional benefit, but also protection against herbivory. A natural population of *S. minor* in northeast Florida was selected to test response to prey and fertilizer nitrogen in a press-experimental design. Introduced fire ants (*Solenopsis invicta*) and ammonium nitrate (NH_4NO_3) were used as prey and fertilizer nitrogen sources, respectively. Treatments included: 1) ant addition; 2) fertilizer addition; 3) ant addition/fertilizer addition; 4) no ants/no fertilizer; 5) control. Treatments were administered biweekly and morphological characteristics and herbivory were measured monthly from April-November 2012. Results indicated no significant treatment effects on plant performance and morphological characteristics, except for a significantly greater number of flowers displayed by the nutrient-deprived group ($p < .005$). Herbivory by *Exyra semicrocea* also showed a marginally significant negative effect on the tallest pitchers per ramet. Since nitrogen is primarily stored by pitchers and allocated to new growth in the following growing season, the predictive power of this study may be limited. However, increased flowering rate in the nutrient-deprived group suggests that plants were induced to flower from nutrient stress. Also, a burn at the beginning of the study likely influenced nutrient availability and plant response to experimental treatments. In conclusion, stress may have occurred from both fire and nutrients, and *S. minor* showed resistance and poor response to nitrogen addition.

INTRODUCTION

History and Background

Plants are one of the most diverse and ancient group of organisms on the planet. Plants account for approximately 22% (≈308,000 species) of extant species (Strong *et al.*, 1984). Diversity of an arthropod community is also influenced by plant diversity (Siemann *et al.*, 1998). Various relationships have evolved between plants and arthropods, such as pollination, seed dispersal, galling, herbivory, ant-protection, myrmecotrophy and insectivory (Bronstein, 1998; Bronstein *et al.*, 2006). However, symbiotic relationships are not often absolute, nor symmetrical, and the degree to which interactions occur, whether mutual, commensal or parasitic, may be difficult to define as transitional ecological roles and functions are examined (Holland and DeAngelis, 2009). Relationships between carnivorous plants and arthropods have been an area of ongoing debate and intrigue. The earliest fossil records of carnivorous plants include pollen of *Aldrovanda* from the Eocene (≈55-34 mya) and Droseraceae from the Miocene period (≈24-5 mya) (Pietropaolo and Pietropaolo, 1999). In 1576, illustrations of pitcher plants belonging to the genus *Sarracenia* were documented in *Nova Stirpium Adversaria* by l'Obel (Romanowski, 2002). Carnivorous plants exist across the globe and have developed unique strategies that allow them to take advantage of available resources and survive in nutrient-poor areas such as bogs or seepage savannas, where competition with other plants is low. Basic morphological observations have suggested that insects benefit these carnivorous plants by providing nutrients such as nitrogen or phosphorous (Plummer and Kethley, 1964). Many studies have investigated the function and purpose of modified leaves in carnivorous plants and whether or not these plants truly depend on insect prey for essential nutrients such as nitrogen, or whether root uptake of nitrogen is sufficient to meet their metabolic needs. Reputable evidence for botanical carnivory came with the discovery of *Dionaea muscipula* (Venus flytrap) and supporting communication between John Ellis and Carl Linnaeus in the mid-18th century (Barthlott *et al.*, 2007). In the 19th century, the association between botanical carnivory and nutrient-deficient habitats was duly noted (Darwin, 1971; 1893 edition revised by Francis Darwin). The ability to utilize both photosynthesis and insect prey for nutrients should provide carnivorous plants with a competitive advantage in nutrient-poor substrates and allows them to exploit niches incapable of being occupied by most plants.

Carnivorous plants and myrmecophytes are exceptional examples of how plants have adapted to limited resources and developed unique relationships with insects to obtain nutrients. Myrmecophytic plants are considered those which harbor ants in a specialized structure which ultimately absorbs nutrients from the ants' debris piles. In comparison, Givnish *et al.* (1984) proposed a definition for carnivorous plants with two requirements: nutrients are absorbed from dead animals on tissue surfaces which contribute to increased plant growth or fitness; and plants must have a unique adaptation or strategy to allocate resources such that the primary result is to attract, capture and/or digest prey. Ants may serve as an indirect nutritional source to myrmecophytic plants whereby the plants absorb nutrients from ant waste products (Thompson, 1981) or as a direct source of nutrition for carnivorous plants (Moon *et al.*, 2010). Both myrmecophytic and insectivorous plants have evolved the ability to gather nutrients from environments with low levels of available soil nutrients. Prey capture is believed to provide a supplemental source of nitrogen. Furthermore, insectivorous plants have a relationship with ants that is mainly documented as antagonistic, such that the ants are used solely as prey, in contrast to myrmecophytic plants which represent a mutualistic relationship with ants. In a myrmecophytic plant, specialized structures benefit the ants by providing potential food resources, in addition to housing and shelter where colonies can safely thrive (Thompson, 1981; Givnish *et al.*, 1984). Myrmecophytic plants are also protected by ants against natural enemies (Brontstein, 1998; Bronstein *et al.*, 2006). In the hooded pitcher plant, *Sarracenia minor*, ants have been demonstrated to not only provide nutritional benefit, but also protection against herbivory by *Exyra semicrocea* caterpillars (Moon *et al.*, 2010). Regardless of proposed differences, insectivorous and myrmecophytic plants share similar life histories and nutrient requirements. Both types of plants are generally perennial, grow in substrates where nutrient levels are low, and derive nitrogen from prey or debris (Thompson, 1981). The variable roles of insects and degrees of interaction between carnivorous plants and potential insect prey are areas of ongoing research. Measurement of insect capture efficiency and allocation of nutrients towards expression of carnivorous or photosynthetic characteristics has also received more recent attention.

In order for botanical carnivory to become favored, benefits of carnivorous structures must outweigh production costs. A trade-off exists whereby energy must be appropriately allocated towards production of carnivorous versus photosynthetic structures. If the nutrients provided by insects via carnivorous structures are insufficient then enhancement of photosynthetic structures must become the primary strategy for survival. In contrast, if sufficient nutrients are obtained from carnivorous structures then energy will likely be allocated towards greater carnivory expression. Carnivorous structures are modified leaves or roots which are conducive for attracting and trapping prey. Prey are consequently digested and absorption of organic nutrients, especially nitrogen, enhances survival of the plant. Multiple evolutionary lineages of botanical carnivory are hypothesized to have occurred as an adaptation to high-light, wet and nutrient-poor habitats (Thompson, 1981; Givnish *et al.*, 1984; Ellison and Gotelli, 2001; Farnsworth and Ellison, 2008; Ellison and Gotelli, 2009). Sites where carnivorous plants are typically found are N-limited (Givnish, 1989; Ellison and Gotelli, 2001; Karagatzides *et al.*, 2009) and include habitats such as bogs, peaty swamps, banks of streams (Thompson, 1981; Givnish *et al.*, 1984), seepage swamps and fens (Butler and Ellison, 2007) and seepage savannahs (Hermann, 1995; Meyer *et al.*, 2001). The relationship between a carnivorous plant and its insect visitors must be balanced such that consumption of beneficial pollinators as prey is avoided. Traps and flowers exhibit a spatial and temporal separation whereby flowers mature before traps or flowers are elevated above traps on elongated petioles. In aquatic carnivorous plants, such as *Utricularia spp.*, the traps, or modified roots, are submerged while the flowers are emergent. In terrestrial pitcher plants and butterworts the flowers mature above opened traps (Zamora, 1999). The advantage of producing carnivorous structures is closely related to available nutrients and mechanisms of energy allocation which enhance survival and fitness.

The specialized morphology of carnivorous plants may selectively capture prey and reflect available habitat resources for a particular environment (Ellison and Gotelli, 2009). In dry environments, myrmecophily, a mutualistic relationship with ants, is favored over carnivory (Thompson, 1981). Photosynthetic rates are often low in carnivorous plants (Small, 1972; Méndez and Karlsson, 1999; Butler and Ellison, 2007) and carnivory provides nutritional benefits that are independent of photosynthesis (Ellison and Gotelli, 2001). Furthermore, Givnish *et al.* (1984) designed a cost-benefit model that predicted botanical carnivory to be favored in nutrient-poor, high-light, moist environments, which Benzing (2000) later expanded to include nutrient tradeoffs through litter. Analysis of the carbon and nitrogen tissue content could indicate the degree to which investment of photosynthetic and carnivorous structures contribute towards survival (Ellison and Gotelli, 2009; Karagatzides *et al.*, 2009). Thus, the ratio of C:N in plant tissues may pose as a useful measurement of carnivory expression, in addition to comparison of carnivorous and photosynthetic morphology (Ellison and Gotelli, 2002; Moon *et al.*, 2008; Moon *et al.*, 2010).

Trapping Mechanisms

Molecular systematics has revealed a high level of trap convergence among carnivorous plants (Ellison and Gotelli, 2009). Trapping mechanisms are considered either active or passive, depending on the response mechanisms to stimuli by insect visitors. Active traps have “hairs” which act as triggers and respond to stimuli by enclosing prey within the modified leaf. Passive traps utilize directional hairs or sticky resin to ensure capture and prevent escape of prey. Examples of active traps are those exhibited by the Venus flytrap (*Dionaeae*) and bladderwort (*Utricularia*). Passive traps are displayed in pitcher plant genera (*Sarracenia, Nepenthes, Heliamphora, Darlingtonia, Cephalotus*), sundews (*Drosera*) and butterworts (*Pinguicula*) (Pietropaolo and Pietropaolo, 1999; Romanowski, 2002; Schnell, 2002; Barthlott *et al.*, 2007; McPherson, 2007). Furthermore, passive traps are divided into flypaper (sticky) traps, which are found in Droseraceae, Drosophyllaceae and Roridulaceae, and pitfall traps, which are found in Nepenthaceae, Cephalotaceae and Sarraceniaceae (Ellison and Gotelli, 2009). Within these families, four genera of pitcher plants (*Sarracenia, Nepenthes, Darlingtonia, Cephalotus*) have juveniles with nonfunctional pitchers which derive nitrogen from older pitchers (Schulze *et al.*, 1997). Non-pitcher, photosynthetic leaves, termed phyllodia, are also produced by *Sarracenia spp*. (Fig. 1, 2; Givnish *et al.*, 1984; Pietropaolo and Pietropaolo, 1996; Ellison and Gotelli, 2002; Barthlott *et al.*, 2007). In *Sarracenia spp.*, pitcher traps are divided into four zones (Fig. 3). Zone 1 is designated as the pitcher hood. The hood has interior, superficial hairs which point inward to facilitate prey movement towards the pitcher tube. The hood may be brightly colored in the ultraviolet spectrum as a visual cue to insects. Non-pigmented spots, or fenestrations, which act as light windows that insects may perceive as a method of escape, are also present on the hood. Zone 2 is the lip, mouth and neck area. The lip, often referred to as the nectar roll, may be brightly colored and consists of nectaries and a smooth waxy surface. Zone 3 is the smooth waxy section of the tube which offers no grip as insects plummet to the bottom digestive zone. This zone also contains digestive enzyme glands. *Sarracenia spp.* are known to produce amylase, esterase, lipase, phosphatase and protease enzymes (Barthlott *et al.*, 2007) which aid digestion of prey and release nutrients readily absorbed by plant tissue. Zone 4 is the digestive zone which is lined with downward pointing hairs and is where usable nutrients from prey are digested and absorbed. The pitcher tube may be filled with fluid where prey drown and sink to the bottom of the tube and final breakdown by enzymes and bacteria occurs (Pietropaolo and Pietropaolo, 1996; Romanowski, 2002).

To further enhance prey attraction, pitcher plants are equipped with both floral and extrafloral nectaries (EFN) (Dress *et al.*, 1997; Newell and Nastase, 1998; Plachno, 2007). Insects receive nutritional benefits of amino acids and sugars from nectar of *S. purpurea* (Dress *et al.*, 1997). Extrafloral nectaries are most dense around the lip of the pitcher. Prey are attracted to the nectar on the smooth, waxy lip where they may slip and fall into the digestive fluid of the pitcher.

Inquiline Community

Pitcher leaves provide refugia and nutritional resources for micro- and macrofauna. In pitchers filled with fluid, such as rain water, a microcosm is created whereby some invertebrates utilize space and nutrients from decomposing prey. This assemblage of organisms is referred to as the inquiline community, or phytotelmata. Inquiline community members of *S. purpurea* may include bacteria, mites, midges, protozoa, rotifers and dipteran larvae (Fish and Hall, 1978; Bradshaw and Creelman, 1984; Heard, 1994; Kneitel and Miller, 2002; Mouquet *et al*., 2008; terHorst, 2010). Copepods and cladocerans have also been observed inside pitchers (Kneitel and Miller, 2002). Detritus is broken down by bacteria, mites and midges, and protozoa and rotifers in turn feed on the bacteria. Bacterial diversity found in *S. minor* pitchers includes strains of *Serratia, Achromobacter, Pantoea, Micrococcus, Bacillus, Lactococcus Chryseobacterium* and *Rhodococcus*, which often arrive from insect vectors (Siragusa *et al.*, 2007). Dipteran larvae compose the top predators in the community; larvae of three dipteran species that have been found to inhabit the pitcher fluid are *Blaesoxipha fletcheri* (Sarchophagidae), *Metriocnemus knabi* (Chironomidae) and *Wyeomyia smithii* (Culicidae) (Fish and Hall, 1978; Heard, 1994; Kneitel and Miller, 2002; Mouquet *et al*., 2008; terHorst, 2010). *Blaesoxipha fletcheri* is restricted to feeding on fresh prey at the water's surface, while *Metriocnemus knabi* feeds on dead prey at the pitcher bottom, and *Wyeomyia smithii* filter-feeds on suspended particulate matter and small organisms including bacteria and protozoa throughout the pitcher fluid (Fish and Hall, 1978; Bradshaw and Creelman, 1984).

Mosquito larvae, *W. smithii*, are considered the keystone predators in this food-web (Mouquet *et al.*, 2008). Within the pitcher the inquiline community is influenced by both temporal and spatial segregation. Spatial segregation is caused by different respiratory mechanisms as well as resource partitioning due to the heterogeneity of food types and feeding behaviors (Fish and Hall, 1978; Kitching, 1987; Naeem, 1988). Temporal segregation occurs due to different developmental and oviposition patterns between *B. fletcheri*, *M. knabi* and *W. smithii* (Fish and Hall, 1978). Succession of organisms composing the inquiline community is also influenced by pitcher age (Fish and Hall, 1978). For instance, Fish and Hall (1978) observed lower abundance of *M. knabi* in youngest and oldest leaves of *S. purpurea*. Thus, competition between inquiline community members is minimized due to the temporal and spatial segregation (Fish and Hall, 1978). Prey nutrients become available to pitcher leaves not only through action by digestive enzymes, but also through decomposition and detritus fractioning as a byproduct of the inquiline food-web (Bradshaw and Creelman, 1984; Heard, 1994). Pitcher plants such as *S. purpurea* are able to directly absorb amino acids (Jones *et al.*, 2009) and nutrients which may be released from decomposed prey and microorganism metabolism (Bradshaw and Creelman, 1984). There is still debate, however, whether competition for nutrients occurs between the pitcher plant and its inquiline community.

Nutrients

Nitrogen is regarded as the nutrient that most limits plant growth (Berendse and Aerts, 1987; Vitousek *et al.*, 1997; Karagatzides *et al.*, 2009). Nitrogen also constitutes the dominant nutrient provided from prey (Shulze *et al.*, 1997). Although prey are a source of phosphorous as well (Plummer and Kethley, 1964), nitrogen has been demonstrated to be the primary limiting nutrient in most plants including *S. purpurea*, while phosphorous acts as a secondary limiting nutrient (Chapin and Pastor, 1995). Recycling and remineralization of nitrogenous compounds is also facilitated by the bacterial diversity found in pitchers (Siragusa *et al.*, 2007). Pitcher plants are capable of absorbing various nutrients from prey including amino acids and peptides through the leaves (Plummer and Kethley, 1964). Competition for soil nutrients varies with habitats and diversity of microbial communities. Thus, it is important to consider the nitrogen cycle and how nitrogen is accumulated and mobilized in soils and assimilated by plants. Anthropogenic effects of agriculture and fossil-fuels should also be considered regarding nitrogen byproducts and nutrient-loading in the environment (Koch and Reddy, 1992; Ellison and Gotelli, 2002). Nutrient loading from atmospheric and agricultural deposition influences the soil N composition and microbial dynamics.

Forms of nitrogen available and usable by plant roots depend upon the soil quality, whether or not the soil is anoxic, and the microbial community composition. In N-limited ecosystems amino acids may regulate nutrient availability due to their high turnover rate caused by microbes (Jones *et al.*, 2009). Dissolved inorganic nitrogen (DIN), such as nitrate (NO_3^-) and ammonium (NH_4^+), are directly absorbed by roots and rhizomes; whereas, dissolved organic nitrogen (DON), such as amino acids, proteins and peptides, must go through the process of nitrification or mineralization in order for roots and rhizomes to utilize the nitrogen (Jones *et al.*, 2005). Sources of nitrogen include precipitation (dissolved NH_4^+ and NO_3^-), mineralized N from prey, potential N present in soil or substrate, and N stored by the plant (Ellison and Gotelli, 2007). Many terrestrial ecosystems contain soils with greater than 90% of their nitrogen bound in organic form, of which amino acids represent 20-40% (Senwo and Tabatabai, 1998). *Sarracenia spp.* absorb minerals and amino acids from digestion of prey protein (Pietropaolo and Pietropaolo, 1996), and *S. purpurea* has been shown to take up amino acids directly (Jones *et al.*, 2009). Roots and pitchers of *S. purpurea* are capable of utilizing NO_3^- due to the presence of nitrate reductase (Butler and Ellison, 2007). Species of Sarraceniaceae in North America such as *S. purpurea* have pitchers that account for the greatest uptake of nitrogen, followed by the roots and rhizomes. Stored N provides the sink by which growth occurs and pitchers are produced. Assimilated and stored nitrogen is then translocated from senescing pitchers into new pitcher biomass, thereby conserving nutrients and amplifying prey capture through carnivory expression rather than production of photosynthetic tissue (Butler and Ellison, 2007). Data from Ellison and Gotelli (2001) showed that dependence on insect-derived nitrogen may increase in some carnivorous plant species as more elaborate carnivorous structures are produced. Efficiency of insect capture and associated nutrients influences energy allocation and carnivory expression. Available nutrient pools also impact uptake and storage in aboveground and belowground biomass.

Sarracenia minor

Carnivorous plants may be important indicators of long-term environmental change because their decline may signal detrimental impacts of chronic N deposition (Ellison and Gotelli, 2001). Much work has been done on the nutrient and prey dynamics of *Nepenthes spp.* (Moran, 1996; Schulze *et al.*, 1997; Ellison and Gotelli, 2001; Bohn and Federle, 2004) and *S. purpurea* (Heard, 1998; Newell and Nastase, 1998; Deppe *et al.*, 2000; Ellison and Gotelli, 2002; Gotelli and Ellison, 2002; Kneitel and Miller, 2002; Wakefield *et al.*, 2005; Atwater *et al.*, 2006; Butler and Ellison, 2007; Mouquet *et al.*, 2008; Karagatzides *et al.*, 2009), but only a limited number of studies have investigated the hooded pitcher plant, *S. minor* (Plummer, 1963; Meyer *et al.*, 2001; Beaulac *et al.*, 2002; Siragusa *et al.*, 2007; Moon *et al.*, 2008; Moon *et al.*, 2010). *Sarracenia minor* is a Florida state-threatened species (Wunderlin and Hansen, 2008; USDA, 2012) and is also a potential indicator species of freshwater wetlands (Meyer *et al.*, 2001; Beaulac *et al.*, 2002). The range of *S. minor* is limited to the southeast United States (Florida, Georgia, South Carolina, North Carolina) (USDA, 2012) and populations have been documented as far south as the Everglades (Romanowski, 2002). *Sarracenia minor* is a facultative wetland plant (Wunderlin and Hansen, 2008) and populations are known to inhabit seepage savannahs (Hermann, 1995; Meyer *et al.*, 2001), bogs and fens (Pietropaolo and Pietropaolo, 1996; Moon *et al.*, 2010) and moist and intermediate pine-barrens (Plummer, 1963). *Sarracenia minor* is an herbaceous perennial which reproduces both asexually and sexually (Pietropaolo and Pietropaolo, 1996; Barthlott *et al.*, 2007) and in northeast Florida produces an average rosette of 5-20 pitchers (Moon *et al.*, 2010). Fenestrations, nectar, waxy cuticles and downward pointing hairs are utilized to entice prey and prevent escape, while digestive enzymes and bacteria in the pitcher liquid are used to break down captured prey (Pietropaolo and Pietropaolo, 1996; Schnell, 2002; Barthlott *et al.*, 2007; McPherson, 2007).

A net benefit may exist for both plants and prey through a balance of consumption and defense that leads to a selectively favored relationship (Rutter and Rausher, 2004; Bronstein, 2006; Moon *et al.*, 2010). Regarding prey capture within Sarraceniaceae, ants, beetles, wasps, flies, crickets and spiders fall victim to pitchers (Pietropaolo and Pietropaolo, 1996; Beaulac *et al.*, 2002), but ants account for the majority of attracted (Newell and Nastase, 1998) and captured insects (Beaulac *et al.*, 2002; Barthlott *et al.*, 2007; Ellison and Gotelli, 2009; Moon *et al.*, 2010). *Sarracenia minor* is hypothesized to be a specialist myrmecophage (Givnish, 1989) and the red imported fire ant, *Solenopsis invicta,* has been observed as the major ant prey of *S. minor* in the southeastern United States (Ellison and Gotelli, 2009). However, fire ants were not found in *S. minor* pitchers at a study site in Duval County, FL (Moon *et al.*, 2010). Moon *et al.* (2010) demonstrated that increased ant attendance to *S. minor* not only provided direct nutritional benefits, but also reduced plant damage from herbivory by *Exyra semicrocea* caterpillars. Nutrient and insect community dynamics of *S. minor* are not completely understood, but further investigation may influence the approach to future research and design of conservation management plans for carnivorous plants and their ecosystems.

Insect prey is proposed to be the most important source of nutrients for carnivorous plants and assimilation of these nutrients directly affects expression of carnivory. However, if carnivorous plants show positive response to root-derived nutrients then conservation programs may be designed which incorporate carnivorous plant species, such as *S. minor*, as potential candidates for reintroduction. The goal of this study was to examine the effects of prey-derived nitrogen by pitchers compared to root uptake of fertilizer nitrogen on performance and fitness of the hooded pitcher plant, *S. minor*, through an in-situ press-experimental design. Plants subjected to prey addition were hypothesized to show enhanced expression of carnivory, plant performance and greater fitness rates. Plants that received NH_4NO_3 fertilizer were hypothesized to display a greater dependence on photosynthetic structures such that carnivory expression would decrease alongside plant performance and fitness.

METHODS

This study was conducted along a boundary of McGirt's Creek Park, Jacksonville, FL (N: 30^{O}13.432'; W: 081^{O}46.965') and data were recorded from April-November 2012. The site is approximately 65m x 20m and situated within a powerline corridor owned by Jacksonville Electric Authority (JEA). Site selection was based, in part, because it is a semi-protected location, and it contains a large, healthy population of *S. minor*. The plot is bordered by largely undisturbed mesic pine-flatwoods and represents a wet prairie community with species of *Utricularia, Aster, Cicuta, Coreopsis, Eriocaulon, Helianthus, Hypericum, Lachnanthes, Liatris, Lilium, Nephrolepis, Polygala, Rhexia, Solidago* and *Xyris*. The canopy is completely open and the corridor has a history of regular disturbance from mowing approximately twice per year by JEA. However, the study site is marked off as a research site and has not been mowed for multiple seasons. In order to clear overgrown vegetation, we requested that JEA mow the site once in late July 2011. Pitcher plants recovered promptly after the mow. In early March 2012, an accidental fire occurred along sections of the powerline corridor and the site was scorched to bare earth (Fig. 4). Subsequently, the population of *S. minor* consisted of similar sized ramets with young or unopened pitchers, many of which had newly produced flowers or buds. Ramets were then haphazardly selected and randomly assigned to treatments.

Experimental Field Design

Nitrogen sources chosen to test the effects of prey and fertilizer on plant performance were fire ants (*Solenopsis invicta*) and ammonium nitrate (NH_4NO_3), respectively. *Solenopsis invicta* was used as the prey addition nitrogen source because ants constitute the vast majority of *S. minor* prey (Givnish, 1989; Beaulac *et al.*, 2002; Barthlott *et al.*, 2007; Ellison and Gotelli, 2009), and also due to their abundance at the site (Stiles and Jones, 2001; Lubertazzi and Tschinkel, 2003) and prevalence in open canopy and disturbed habitats (Menzel and Nebeker, 2008; Epperson and Allen, 2010). The corridor contained numerous fire ant colonies both within and outside the study area. Ammonium nitrate (NH_4NO_3) was used as the fertilizer nitrogen source due to the solubility and nitrogen ions in NH_4^+ and NO_3^- which are readily absorbed by plant roots. NH_4NO_3 has also been used as a nitrogen source in previous studies of *S. purpurea* (Butler and Ellison, 2007; Karagatizides *et al.*, 2009).

Plants were selected haphazardly and randomly assigned to treatments. Press-experimental treatments were: 1) + Ants; 2) + Fertilizer; 3) + Prey/+ Fertilizer; 4) No Ants/No Fertilizer; 5) Control. Each treatment contained 15 replicates, for a total N=75 plants. A secondary control to standardize soil moisture was administered to all plants in treatments that did not receive fertilizer solution using an equal volume of roH_2O, which follows the protocol used in previous studies (Butler and Ellison, 2007). For the prey-addition treatment groups, 20 ants (7mg) were administered biweekly for a total of 40 ants (14mg)/month to the tallest pitcher/ramet. The number of ants added to each pitcher was derived from previous research and analysis of *S. minor* pitcher contents which indicated a mean catch of 125 ants per pitcher over a three month active period (Beaulac *et al.*, 2002). A stock solution of organic NH_4NO_3 was used to produce a 10% N concentration that represented equivalent nitrogen content to that of *S. invicta* (Table 1). The 10% N solution was also administered biweekly in doses of 50mL for a total of 100mL/month. Applying nutrient solution on a biweekly rate is a relatively common method (Ellison and Gotelli, 2002). The N stock solution was applied in monthly doses of 100mL which is approximately equal to the nitrogen content of 14mg of *S. invicta*. All pitchers of plant ramets in manipulated treatments 1-4 were also plugged with cottonballs to prevent ambient prey from being captured by the plants (Fig. 5). Cotton was replaced as needed and appropriately sized pieces of cotton were used to plug pitcher mouths. Cotton occasionally became damp from rain and was gently removed and replaced as needed to prevent rotting of plant tissue. Various studies have used cotton (Moran and Moran, 1998) and other materials to plug pitchers such as cheesecloth, wire mesh, or glass wool (Chapin and Pastor, 1995; Ellison and Gotelli, 2002).

Individual ramets were marked using wire flags as well as aluminum tags and orange flagging which were tied loosely around the ramet. An additional loop of orange flagging was used to designate the tallest pitcher being measured. The orange flagging helped to keep measurements of ramets and pitchers consistent, since a neighboring ramet would often encroach and new taller pitchers would mature rapidly. Data recorded for each pitcher ramet included number of pitchers, phyllodia and flowers. Measurements of pitcher height and width, keel width and mouth diameter were taken on the tallest pitcher of each replicate (Fig. 1). Height of the tallest pitcher was measured from the ground to the apex of the hood with a ruler to the nearest millimeter (Moon *et al.*, 2008; Moon *et al.*, 2010). Pitcher width, keel width, and mouth diameter were measured at the widest point to the nearest .01mm using digital calipers. Diameter of the pitcher mouth was measured directly above the lip between the vertices where the hood begins. Herbivory was measured as a count of the number of *Exyra semicrocea* caterpillar galleries per tallest pitcher per ramet, and total number of pitchers per ramet with galleries. Data were recorded once every four weeks.

Ant Collection and Analyses

Collection of *S. invicta* started in summer and fall 2011, and continued throughout the project as needed. Ants were collected using an aspirator, stored in plastic vials and frozen at 0^{o}C until sorted and dried. A sit-and-wait tactic was used at *S. invicta* mounds, but a petri dish with sugar-water occasionally proved successful to bait ants. In the lab, a metal splatter screen, paper plate and paintbrushes were used to separate ants from loose soil pebbles and plant material. Sorted ants were then heated at 40°C for a minimum of 72 hours to eliminate water mass. Dried ants were fed to pitchers and used for ant mass and nitrogen analysis.

Dried ants were weighed to the nearest 0.1mg using an analytical balance (Denver Instrument Company, TR-204). Linear regression was used to describe the relationship between ant quantity and mass. Eight groups of ants (5, 10, 15, 20, 25, 30, 35, 40), each with five replicates, were counted and weighed. Means of each ant group were used to establish a regression equation (Fig. 6, $y = 0.359x - 0.385$, $r = .950$), with ant quantity as the independent variable. The correlation between ant quantity and mass was highly statistically significant ($F_{7, 39} = 70.484$, $p < .001$). The equation was then used to calculate the mass of 40 ants (14mg) so that ants could subsequently be weighed in the lab for use in the field. Note that the mass of a specified quantity of ants as calculated using the equation was within a 2% difference from the actual ant group mean. Dried ants were then stored in glass screw-top vials (each with 7mg ants) and placed in a desiccant chamber until required in the field.

Ant nitrogen content was analyzed to determine nitrogen content as a percent. Ants were homogenized with a Wiley Mill and combusted in a CHNS/O Analyzer (PerkinElmer, Series II CHNS/S Analyzer 2400). Four replicates of ant groups, each with 40 ants, were homogenized and each group was divided into two sub-replicates. Sub-replicates contained 2mg of homogenized ants (as set by CHNS/O Analyzer protocol). Means of each replicate were used to calculate a final mean of 10.4% nitrogen (Table 1). Thus, using molarity and dilution formulae, a 10% N-fertilizer solution was created using the stock NH_4NO_3 solution. A one-way ANOVA with a Tukey's HSD post-hoc test and Bonferroni correction was used to test if any variation of ant nitrogen occurred. As expected, the nitrogen content of ants did not show a significant statistical difference ($F_{3, 7} = 4.977$, $p = .078$).

Statistical Analyses of Treatments

Statistical analyses and figures were generated using SPSS and SigmaPlot, respectively. Preliminary and post-treatment data of pitcher, phyllodia and flower number, as well as, pitcher height, pitcher width, keel width and pitcher mouth diameter were analyzed with a one-way Analysis of Variance (ANOVA) with a Tukey's HSD post-hoc test and Bonferroni correction. Pre-treatment data showed no statistical difference between groups. When data could not be normalized or other assumptions of the ANOVA were not met, data were analyzed non-parametrically using a χ^2-test.

RESULTS

Results of the ANOVA showed that nutrient status produced no significant statistical differences between treatments for number of pitchers ($F_{4, 72}$ = .347, p = .845), number of phyllodia ($F_{4, 72}$ = .292, p = .882), pitcher height ($F_{4, 72}$ = .349, p = .844), pitcher width ($F_{4, 72}$ = .388, p = .817), keel width ($F_{4, 72}$ = .812, p = .522) or pitcher mouth diameter ($F_{4, 72}$ = .481, p = .749). Ranges of means for all treatments were: pitcher number = 5.9-7.9; phyllodia number = 1.1-1.6; flower number = .03-.1; pitcher height = 169.4-186.2; pitcher width = 11.8-13.5; keel width = 12.2-13.9; mouth diameter = 8.7-10.0 (Table 2). Pooled total number of new phyllodia per treatment were also not affected by treatments (Fig. 8, χ^2 = 2.346, df = 4, p > .5). The nutrient-deprived group (No Ants/No Fertilizer) showed the greatest mean number of pitchers, flowers and pitcher mouth diameter, while the control group showed the greatest mean pitcher height, pitcher width and keel width.

No significant treatment effects were shown for the percent change between the minimum and maximum number of pitchers (Fig. 7, $F_{4, 70}$ = .094, p = .984), pitcher height (Fig. 10, $F_{4, 70}$ = 1.485, p = .217), pitcher width (Fig. 11, $F_{4, 70}$ = .581, p = .678), keel width (Fig. 12, $F_{4, 70}$ = .265, p = .900) or mouth diameter (Fig. 13, $F_{4, 70}$ = .635, p = .640). Ant-deprived groups (+ Fertilizer, No Ants/No Fertilizer) generally displayed the lowest percent change of number of pitchers, and greatest percent change for pitcher height, pitcher width, keel width, and mouth diameter.

Analysis of herbivory showed no significant treatment effect for total number of pitchers per ramet with *E. semicrocea* galleries ($F_{4, 70}$ = .250, p = .908) or number of galleries per tallest pitcher per ramet ($F_{4, 70}$ = .515, p = .725). A scaled χ^2-test was also used to detect any trends in totals per treatments. Total number of pitchers with galleries showed no significance (Fig. 14, χ^2 = 1.756, df = 4, p > .5), but marginal significance was detected for total number of galleries per tallest pitcher (Fig. 15, χ^2 = 9.488, df = 4, .05 < p < .1). The control group, which had the greatest mean pitcher height, width, and keel width, also showed the greatest number of galleries per tallest pitcher. Although no significance was detected, plants in treatments deprived of prey (+ Fertilizer, No Ants/No Fertilizer) displayed the greatest total number of pitchers with *E. semicrocea* galleries.

A strong statistical difference was detected for number of flowers per ramet using a scaled χ^2-test (Fig. 9, χ^2 = 16.000, df = 4, p < .005). The χ^2-test was conducted for flower number due to heteroscedastic variances that could not be normalized through data transformation. Plants in the No Ants/No Fertilizer treatment not only produced the most flowers per ramet (Fig. 9, χ^2 = 16.000, df = 4, p < .005) but also new phyllodia per ramet (Fig. 8, χ^2 = 2.346, df = 4, p > .5). Plants in treatments manipulated with ant addition (+ Ants, + Ants/+ Fertilizer) produced the fewest number of flowers but ranked second to the No Ants/No Fertilizer treatment in new phyllodia production. In addition to greatest flowering rate, the No Ants/No Fertilizer group and control group also had the greatest number of *E. semicrocea* galleries per tallest pitcher.

DISCUSSION

Carnivorous plants perform as both producers and consumers and are able to exploit a niche not occupied by most plants. Carnivorous plants have adapted to sunny, wet and nutrient-poor habitats by evolving unique strategies to obtain nutrients from prey (Thompson, 1981; Givnish *et al.*, 1984; Ellison and Gotelli, 2001; Farnsworth and Ellison, 2008; Ellison and Gotelli, 2009). Carnivorous organs must therefore be selectively favored over production costs and photosynthesis. Florida contains a rich biodiversity, including numerous threatened and endangered species (Myers and Ewel, 1990), and the greatest diversity of carnivorous plants in the United States (Hermann, 1995). One *Dionaea sp.,* five *Drosera spp.,* six *Pinguicula spp.,* 16 *Sarracenia spp.* and 14 *Utricularia spp.* are found throughout Florida; this includes one threatened and one endangered *Drosera spp.*, five threatened and one endangered *Sarracenia spp.*, three threatened and two endangered *Pinguicula spp.* The focus of this study, the hooded pitcher plant, *Sarracenia minor*, is a facultative wetland plant and FL-threatened species (Wunderlin and Hansen, 2008). Unfortunately, the wetland habitats where *S. minor* is typically found, such as bogs and seepage savannahs, are sensitive ecosystems which are greatly impacted by anthropogenic activities even outside their borders. In order to help conserve and protect wetland environments in Florida the Warren S. Henderson Wetlands Protection Act was enacted in 1984 which regulates activities in wetlands, including construction, dredging and filling (Smallwood *et al.*, 1985; Beaulac *et al.*, 2002). Carnivorous plants have also been suggested as indicators of N deposition (Ellison and Gotelli, 2001) which may be environmentally detrimental. However, much work has investigated the northern pitcher plant, *Sarracenia purpurea* (Fish and Hall, 1978; Bradshaw and Creelman, 1984; Chapin and Pastor, 1995; Dress *et al.*, 1997; Heard, 1998; Newell and Nastase, 1998; Deppe *et al.*, 2000; Ellison and Gotelli, 2002; Gotelli and Ellison, 2002; Kneitel and Miller, 2002; Wakefield *et al.*, 2005; Atwater *et al.*, 2006; Butler and Ellison, 2007; Mouquet *et al.*, 2008; Karagatzides *et al.*, 2009) and *Nepenthes spp.* (Moran, 1996; Schulze *et al.*, 1997; Moran and Moran, 1998; Bohn and Federle, 2004), but limited research has focused on *S. minor* (Plummer, 1963; Meyer *et al.*, 2001; Beaulac *et al.*, 2002; Siragusa *et al.*, 2007; Moon *et al.*, 2008; Moon *et al.*, 2010). More research is needed to understand community and nutrient dynamics of *S. minor* which may help to design future conservation and management plans that protect carnivorous plant communities and threatened ecosystems.

Despite its negative reputation, the recently introduced fire ant, *Solenopsis invicta*, could have beneficial value for the ant specialist and FL-native and threatened hooded pitcher plant, *Sarracenia minor*. Fire ants are well known for their aggressiveness and negative impact on native invertebrate diversity, especially resident ant communities (Stiles and Jones, 2001; Lubertazzi and Tschinkel, 2003; Menzel and Nebeker, 2008; Epperson and Allen, 2010). However, since ants have been demonstrated to provide both nutrition and protection against herbivory to *S. minor* (Moon *et al.*, 2010), the aggressive *S. invicta* could be a prime benefactor for *S. minor*. Fire ant colonies were prevalent in the powerline corridor and were observed as the dominant ant species at the McGirt's Creek site. Fire ant mounds were often present in close proximity to pitcher plant ramets and ants were frequently observed on pitchers (Fig. 16). Thus, the presence of fire ants would serve as nutritional value to *S. minor*, complemented by protection from herbivory. Various insect prey have been recorded in *S. minor* pitchers, which include ants, beetles, flies, hemipterans, orthopterans, wasps and spiders (Pietropaolo and Pietropaolo, 1996; Beaulac *et al.*, 2002), but ants constitute the majority of attracted (Newell and Nastase, 1998) and captured prey (Beaulac *et al.*, 2002; Barthlott *et al.*, 2007; Ellison and Gotelli, 2009; Moon *et al.*, 2010). Considering the abundance of fire ants at the site, the natural diversity of the arthropod community may be negatively impacted. However, the observed arthropod diversity at McGirt's Creek appeared relatively rich and included members of the orders Coleoptera (families: Buprestidae, Cantharidae, Carabidae, Chrysomelidae, Scarabaeidae), Diptera (families: Calliphoridae, Culicidae), Hymenoptera (families: Apidae, Formicidae, Halictidae, Sphecidae, Vespidae), Hemiptera (families: Cercopidae, Cicadellidae, Pentatomidae), Lepidoptera (families: Erebidae, Hesperiidae, Lycaenidae, Noctuidae, Nymphalidae, Papilionidae, Pieridae, Yponomeutidae), Odonata (families: Aeshnidae, Coenagrionidae, Libellulidae), Orthoptera (families: Acrididae, Gryllidae, Tetrigidae, Tettigoniidae) and Araneae. Furthermore, top-down control by fire ants (Stiles and Jones, 2001) on the herbivorous *E. semicrocea* and orthopterans, as well as spiders which potentially compete with pitchers for prey, may actually benefit *S. minor* populations. If the presence of the introduced fire ant positively influences the survival of a native, threatened species such as *S. minor*, then this introduced species may have positive implications not typically considered.

Although original hypotheses were rejected, disturbance from the mow and burn must be incorporated in the interpretation of results from this study. The mow in July 2011 and accidental fire in March 2012 likely influenced the nutrient dynamics of the site as well as the response of *S. minor* to nitrogen manipulation. Promptly following the fire, pitcher plants were among the first species to resprout. A resprouting strategy implies that energy must be stored in specialized organs (Carpenter and Recher, 1979) such as rhizomes in *S. minor*. Fires have been known to promote plant diversity and ecosystem health (Myers and Ewel, 1990; Glitzenstein *et al.*, 1995) and benefit carnivorous plants by means of reducing competitive vegetation and canopy cover, as well as releasing nutrients (Pietropaolo and Pietropaolo, 1996; Romanowski, 2002; Schnell, 2002; Barthlott *et al.*, 2007; McPherson, 2007). Various nutrients such as phosphorous, potassium and magnesium may play a minor role in plant performance, but nitrogen has been shown to be the primary limiting nutrient for *S. purpurea* (Chapin and Pastor, 1995). Nutrients released by the burn could have created a sink of N for *S. minor* whereby potential treatment effects of prey-N and fertilizer-N became negligible. Burns modify soil nutrient concentrations and often result in a pulse of nutrients, such that pools of inorganic N and P increase (Kutiel and Naveh, 1987; Anderson and Menges, 1997). Pools of NH_4^+ and NO_3^- have been shown to rapidly increase immediately following a burn, and decrease throughout the growing season as plant assimilation and leaching occurs (Lavoie *et al.*, 2010). Furthermore, herbaceous plants have been shown to increase growth and storage following a nutrient flush from ash-soil. Rhizomatal species such as the clover, *Trifolium sativum*, also displayed poor response to available soil nitrogen after a burn (Kutiel and

Naveh, 1987). In light of this evidence, available N potentially contributed to growth or storage in *S. minor* and rendered any additional N provided through ants or fertilizer ineffective.

When plants are deprived of a sufficient supply of external nitrogen, nitrate reserves are rapidly drawn down from tissues (Chapin, 1991). Storage and allocation of nutrients to roots supports development and growth in perennial plants subjected to poor-resource environments (Chapin *et al.*, 1990; Chapin, 1991), and diverting resources to defense or storage will cause slow growth (Chapin, 1991). Butler and Ellison (2007) showed that *S. purpurea* does not rely on roots for N-acquisition and that stored nitrogen in pitchers is translocated to growth in the subsequent growing season (Butler and Ellison, 2007). Thus, detection of any treatment effects may also have been limited in this study since only a single growing season was measured. Increased foliar content of nitrogen and phosphorous from insect prey have also been recorded for *Sarracenia spp.* (Chapin and Pastor, 1995). However, according to the prey-deprivation study by Moran and Moran (1998), nitrogen and phosphorous concentrations in root and leaf tissue showed no significant differences in *N. rafflesiana*; but, foliar reflectance in prey-deprived plants was significantly higher in the photosynthetically active waveband (608-738nm) and reduced at 550nm. Therefore, foliar reflectance may be a more powerful indicator of nutrient stress, especially nitrogen, compared to analyses of nutrient concentrations in tissues (Moran and Moran, 1998).

Following the burn, majority of pitcher plants in the population consequently produced flowers and buds in addition to young and immature, unopened, pitchers. Abrahamson (1984) observed an increased flowering response to fire in various Florida plant species such as *Aristida stricta, Lilium catesbaei, Panicum abscissum* and *Polygala rugellii*, among others. Certain carnivorous plants, such as some *Drosera spp.*, depend on fire to flower or will display an increased flowering rate in response to burns (Pietropaolo and Pietropaolo, 1996). Frequency, intensity and season of fires are also factors that will influence the response and recovery of organisms and ecosystems (Abrahamson, 1984; Knight and

Holt, 2005). Late spring/summer fires often result in a flowering response while winter fires cause a vegetative response (Abrahamson, 1984). The question whether *S. minor* flowered after the burn due to a temporal cue or nutrient factor, such as stress, is open for debate. In the latter scenario regarding nutrient-stress, flowering may have resulted as a survival strategy. Mechanisms which stimulated an increased flowering rate by *S. minor* in the nutrient-deprived group of this study are also speculative due to potential influence by prior disturbance and/or nutrient-stress from fire.

Exposure to various degrees of stress in this study, such as fire, nutrients and herbivory, are factors likely related to treatment responses. Greater flowering rate in the nutrient-deprived treatment group (Fig. 9, No Ants/No Fertilizer) suggests a stress induced strategy for survival. Hormonal balances are altered in response to stressful conditions (Chapin, 1991), and decreased rate of photosynthesis may be caused by reduced stomatal conductance in response to nitrogen stress (Chapin, 1991). Many plant species can be induced to flower from stress factors such as poor nitrogen and nutrition, drought, photoperiod or temperature in order to produce seeds to increase chances of survival (Kolář and Seňková, 2008; Wada and Takeno, 2010). For instance, drought is known to promote flowering in *Citrus spp.* (Monselise, 1985) and both drought and salinity accelerate flowering in the desert species *Mesembryanthemum crystallinum* (Adams *et al.*, 1998). *Arabidopsis thaliana* also displayed an early and increased flowering rate due to nutrient reduction (Kolář and Seňková, 2008). Aside from nutrient-stress, induced flowering from disturbances such as burns must not be overlooked since many species display greater flowering rates directly related to fire (Abrahamson, 1984; Pietropaolo and Pietropaolo, 1996). Control plants also displayed a relatively high rate of flowering, which does not necessarily indicate good health, but may imply that plants were subjected to stress from insufficient nutrients or fire. Results of *S. minor* flowering are supported by the aforementioned evidence which indicates that plants produced more flowers due to stress.

Herbivory on *S. minor* pitchers was caused by both *Exyra semicrocea* caterpillars and orthopterans. Herbivory by *E. semicrocea* caterpillars eventually causes pitcher senescence and was observed as brown epidermal galleries on plant tissue caused by consumption from inside the pitcher (Moon *et al.*, 2008). Herbivory from orthopterans was obvious as tissue damage to pitcher tubes and keels. Control plants showed the greatest number of galleries per tallest pitcher (Fig. 15) along with the greatest mean height, keel width and mouth diameter (Table 2). Moon *et al.* (2008) also observed a positive correlation between herbivory and tallest pitchers of *S. minor*. Thus, increased herbivory on control pitchers is probably accredited to their larger size which designates them as larger targets for *E. semicrocea*. Furthermore, as herbivory increased the growth and flowering rates of *S. minor* decreased (Moon *et al.*, 2008). In contrast, this study showed that treatments with relatively greater levels of herbivory, particularly number of galleries per tallest pitchers, displayed an increased flowering rate. Herbivory is also directly influenced by plant tissue quality. Foliar nutrient concentrations, especially nitrogen, are a driving force of insect parasitism such as galling (Stiling and Rossi, 1996; Stiling and Rossi, 1997; Rossi and Stiling, 1998; Moon *et al.*, 2000). Therefore, herbivory on *S. minor* pitchers, which are N sinks, may be a stress factor partly responsible for slow growth or flowering rate. Although difficult to determine from this study, foliar nitrogen of nutrient-deprived and control groups possibly increased, along with flower production, as a means to enhance carnivory expression and increase chances of survival. In this case, increased flowering rate may have also occurred from stress caused by a combination of nutrient-deficiency and herbivory.

Slow growth and low rates of photosynthesis, in addition to low nutrient uptake capacity, are characteristic of plants in low-resource habitats (Chapin 1980; Grime 1977; Parsons 1968) even when supplied with optimal resources (Chapin, 1991). Results from this study are consistent with previous research on *S. purpurea* which showed no treatment effect of prey addition on morphological and growth characteristics (Wakefield *et al.*, 2005). Furthermore, the use of fertilizer on *Sarracenia spp*. is superfluous for survival and growth (Romanowski, 2002; Butler and Ellison, 2007). Increased flowering rate in the No Ants/No Fertilizer treatment group also denotes nutrient stress. Disturbances from the mow and burn at the beginning of this study are suspected to be major factors that impacted *S. minor* growth and fitness responses. Energy allocation and storage were conceivably influenced by stress and alteration of the available nutrient pools. In conclusion, S*. minor* displays resistance and poor response to nitrogen addition, and would serve as an ineffective species indicator of N-deposition.

Further investigation of soil and inquiline nutrient dynamics, as well as long-term monitoring over consecutive growing seasons, may provide insight towards pitcher plant performance and conservation plans. Measuring effects of various levels of disturbance and stress on carnivorous plants could also help disseminate strategies used for energy storage and allocation. Greenhouse experiments that control ambient soil nutrients and genotypes would also be worthwhile endeavors to help identify mechanisms responsible for growth and fitness patterns.

APPENDIX I: TABLES

Table 1: Mean ± SEM of nitrogen content (%) of fire ants (*Solenopsis invicta*). Final mean of replicates equals 10.4%.

	Group 1	**Group 2**	**Group 3**	**Group 4**
Fire Ant N Content (%)	10.52 ± .055	11.25 ± .045	10.14 ± .275	9.55 ± .570

Table 2: Mean ± SEM of morphological characteristics of *S. minor*. Parameters were analyzed using a one-way ANOVA, except for number of flowers which was analyzed using a χ^2-test (see text for details).

Treatment	**Number of Pitchers**	**Number of Phyllodia**	**Number of Flowers**	**Pitcher Height (mm)**	**Pitcher Width (mm)**	**Keel Width (mm)**	**Mouth Diameter (mm)**
+ Ants	7.0 ± 1.47	1.6 ± .41	$3e^{-2}$ ± .02	176.9 ± 8.08	11.800 ± .8812	13.620 ± .6713	8.652 ± .7240
+ Fertilizer	6.4 ± 1.02	1.1 ± .25	$5e^{-2}$ ± .02	169.4 ± 10.19	12.355 ± 1.0881	12.384 ± .7553	9.215 ± .6926
+ Ants/+ Fertilizer	7.2 ± 1.65	1.3 ± .34	$3e^{-2}$ ± .02	173.2 ± 8.58	12.601 ± 1.0173	13.050 ± 1.1516	9.634 ± .7061
No Ants/No Fertilizer	7.9 ± 1.28	1.4 ± .24	.1 ± .04	175.0 ± 9.92	12.893 ± 1.1240	12.191 ± .7264	9.956 ± .9429
Control	5.9 ± .80	1.3 ± .27	.1 ± .04	186.2 ± 14.54	13.451 ± .7315	13.941 ± .7701	9.560 ± .4030

APPENDIX II: FIGURES

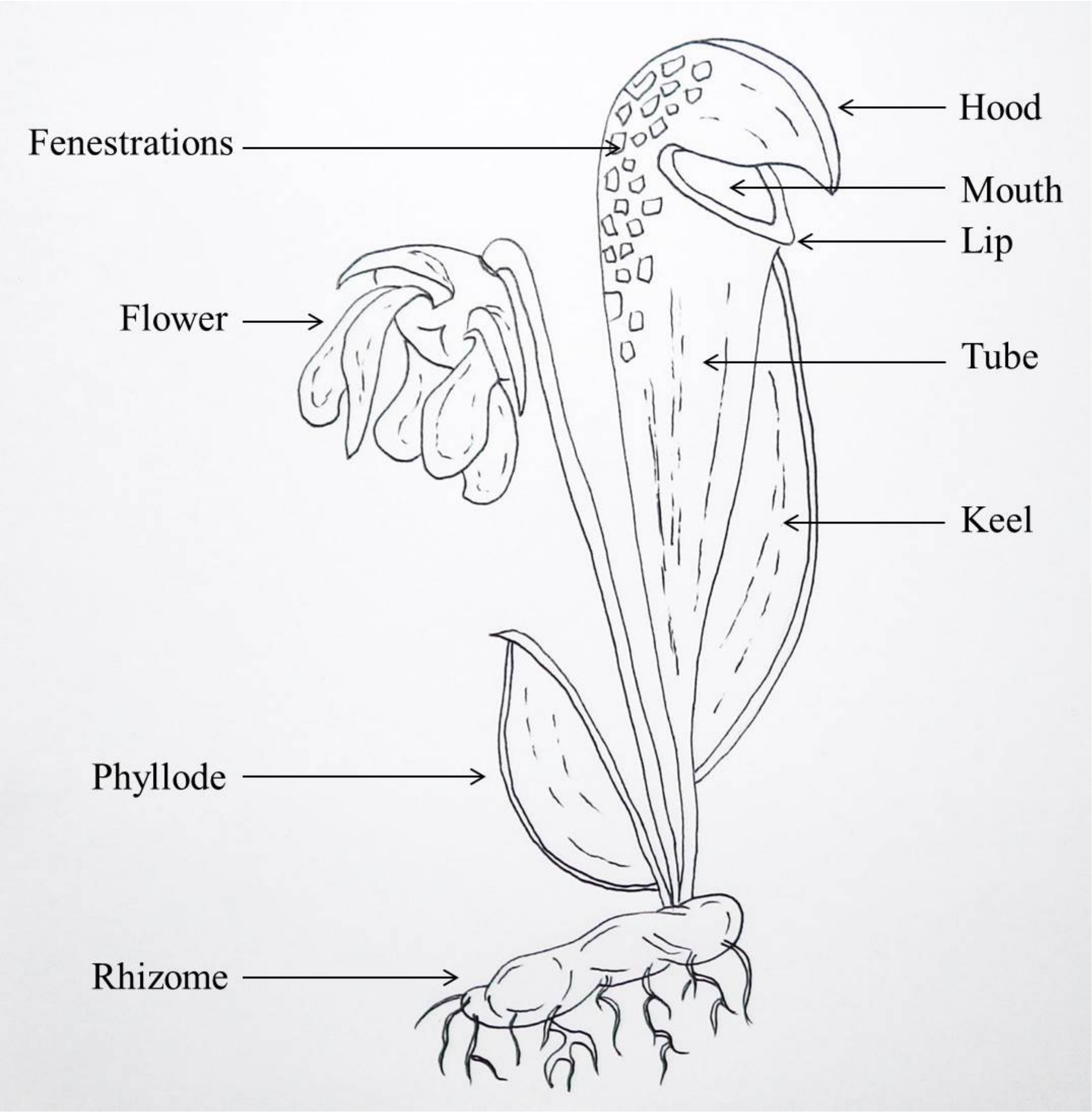

Figure 1: Morphology of the hooded pitcher plant, *Sarracenia minor*. Note photosynthetic phyllode and keel.

Figure 2: Photosynthetic phyllode produced by *S. minor*.

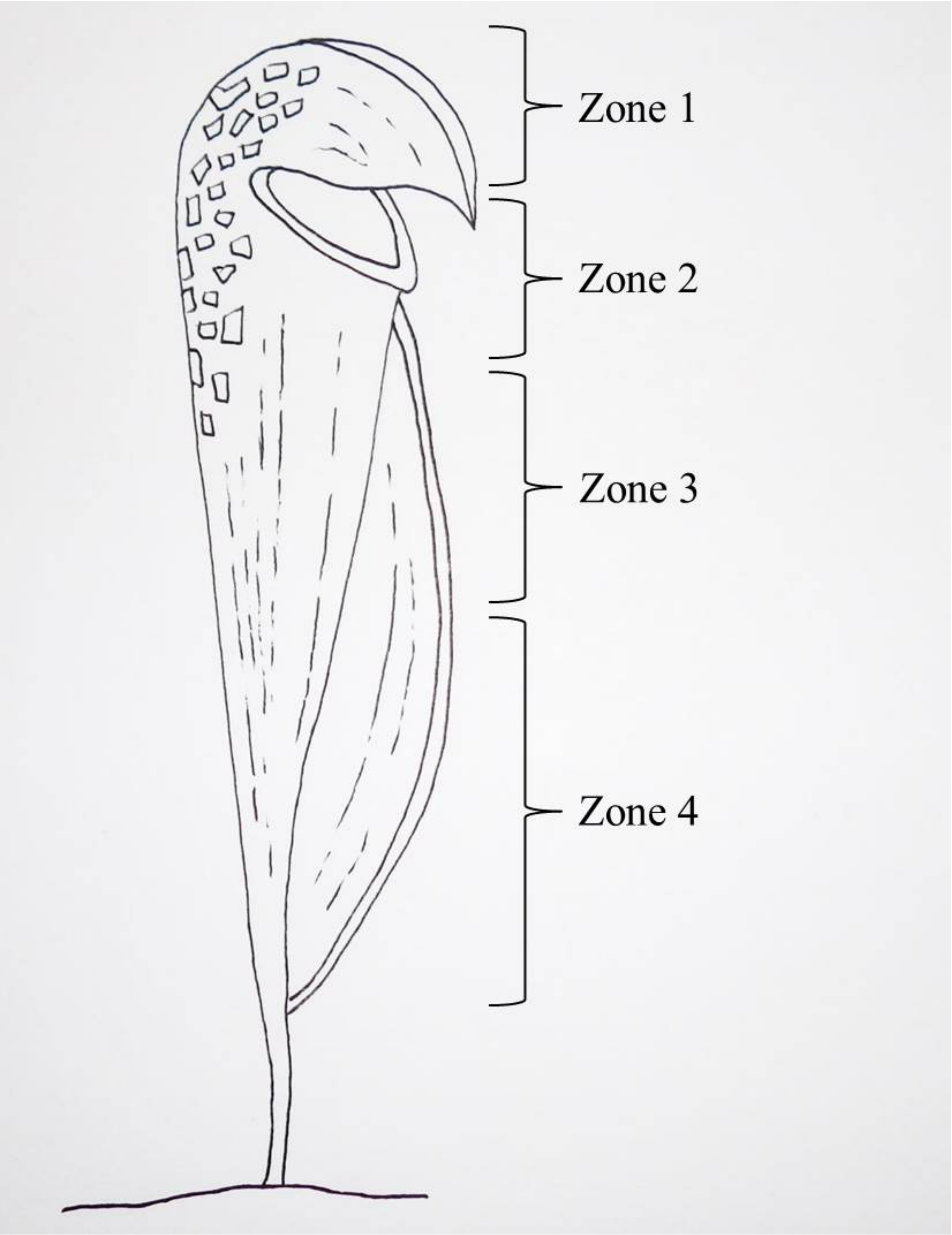

Figure 3: Pitcher plant zones: Zone 1 = hood region with directional hairs and fenestrations; Zone 2 = lip, mouth and neck region with nectar glands; Zone 3 = waxy region with enzyme glands; Zone 4 = fluid filled digestive region with downward pointing hairs.

Figure 4: McGirt's Creek research site after the accidental fire on March 2, 2012.

Figure 5: *Sarracenia minor* pitchers plugged with cotton to control ambient prey capture.

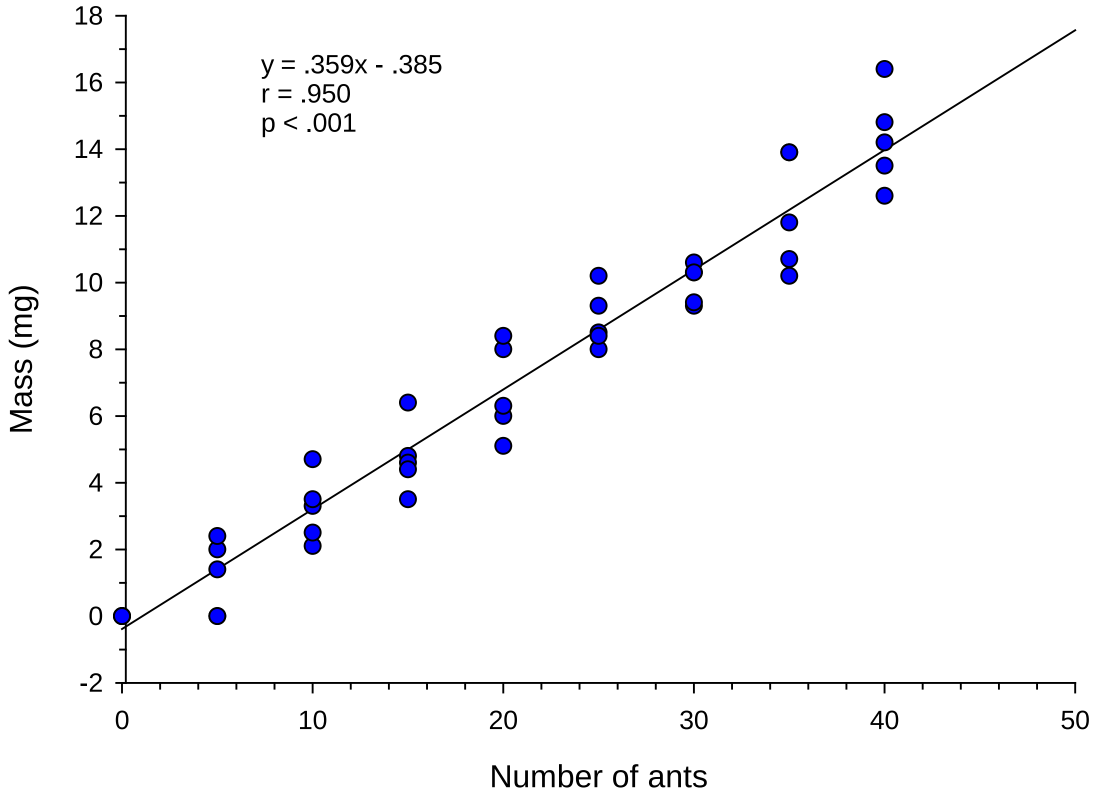

Figure 6: Linear regression of fire ant, *S. invicta*, quantity vs. mass (mg) (y = .359x - .385, r = .950).

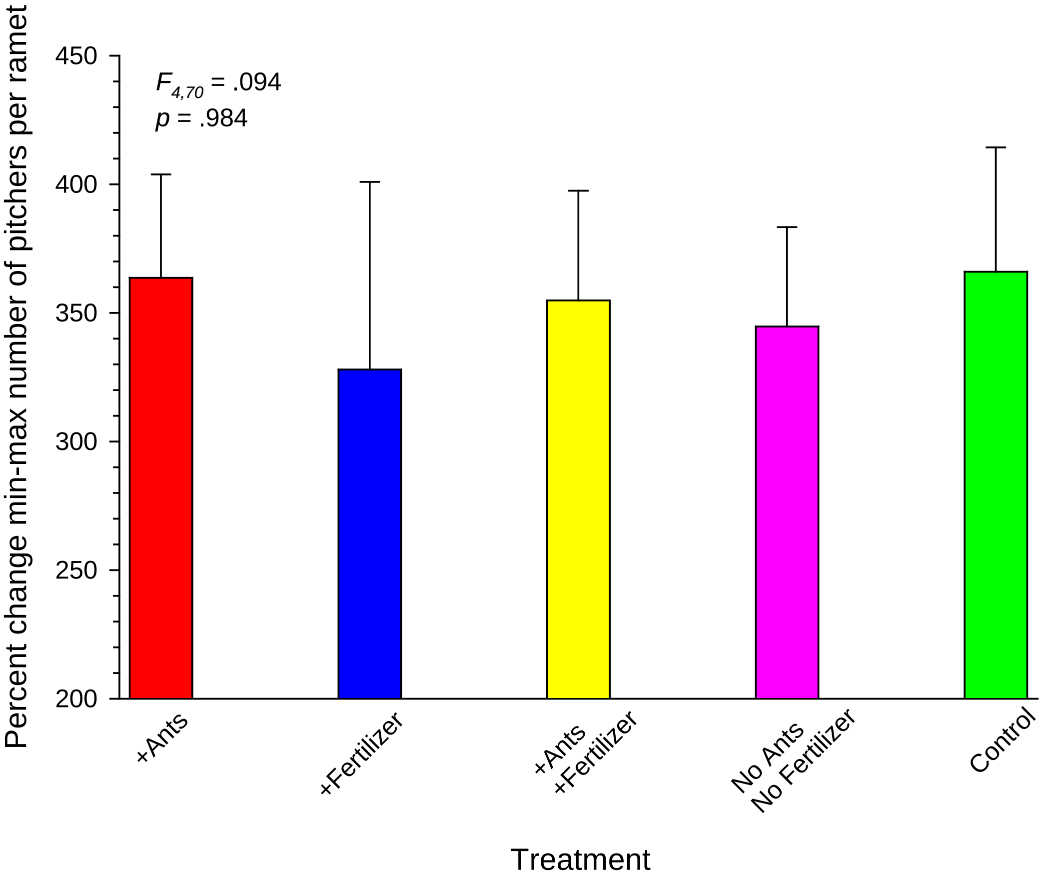

Figure 7: Percent change between the minimum and maximum number of pitchers per ramet.

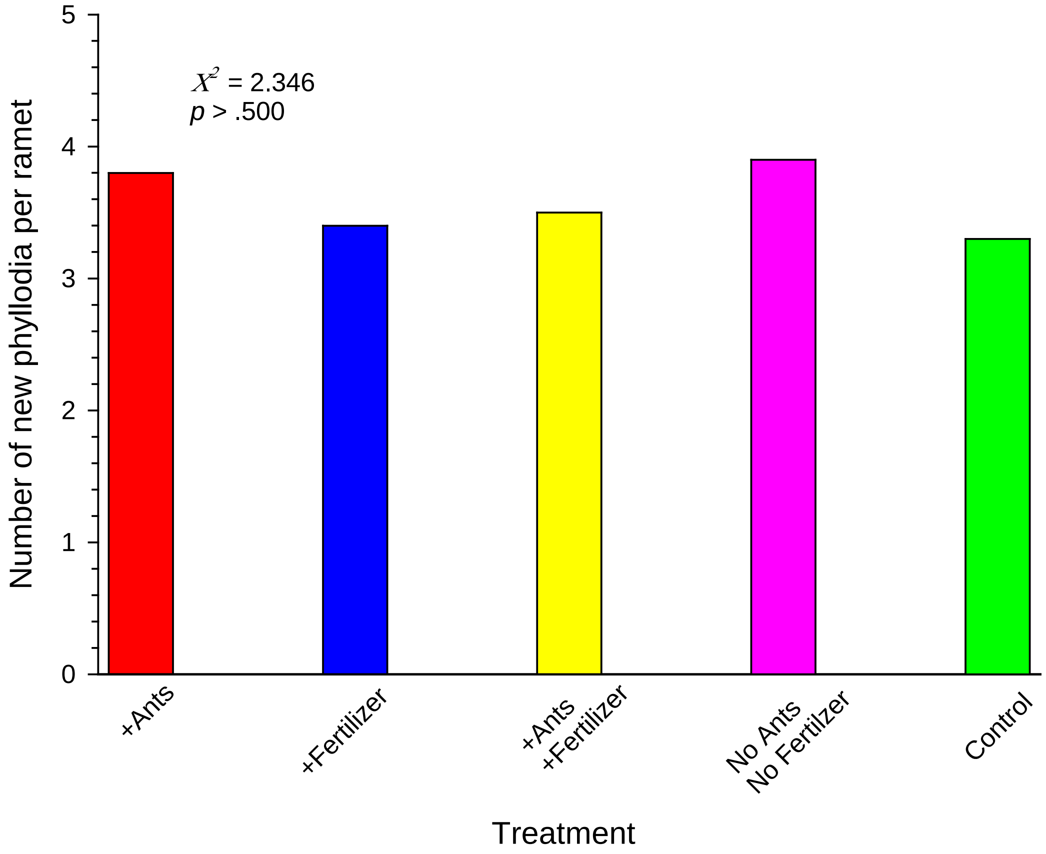

Figure 8: Number of new phyllodia produced per ramet.

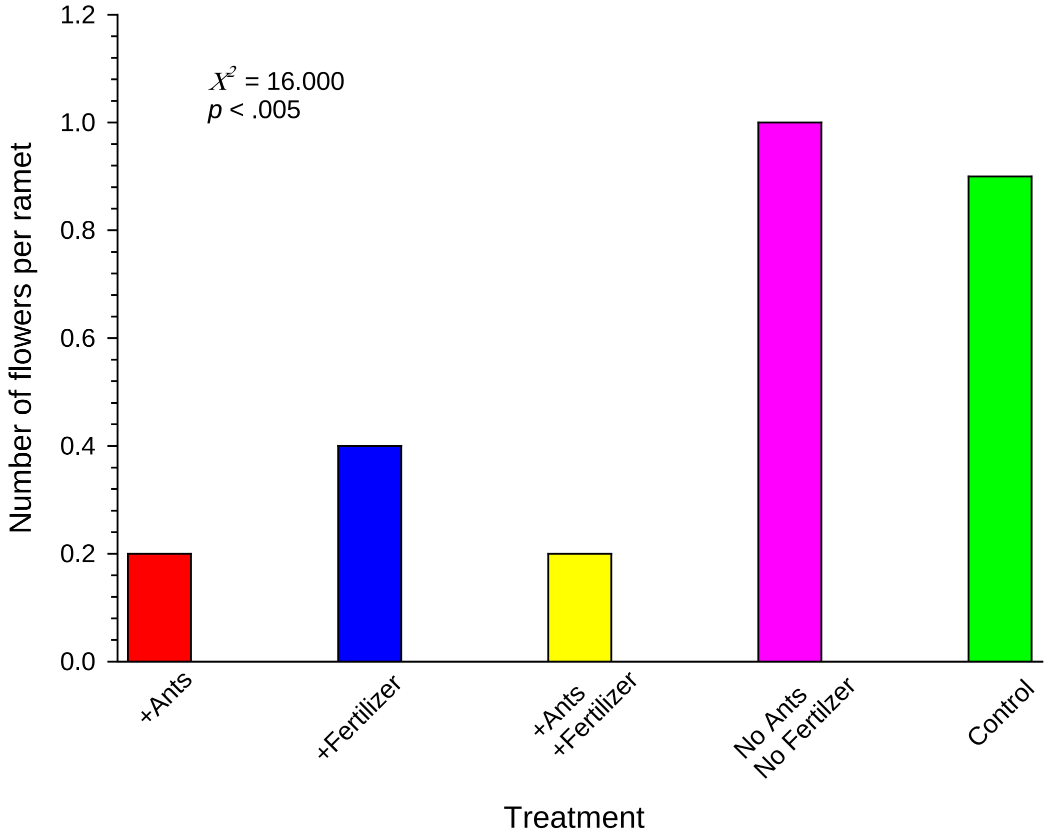

Figure 9: Number of flowers produced per ramet.

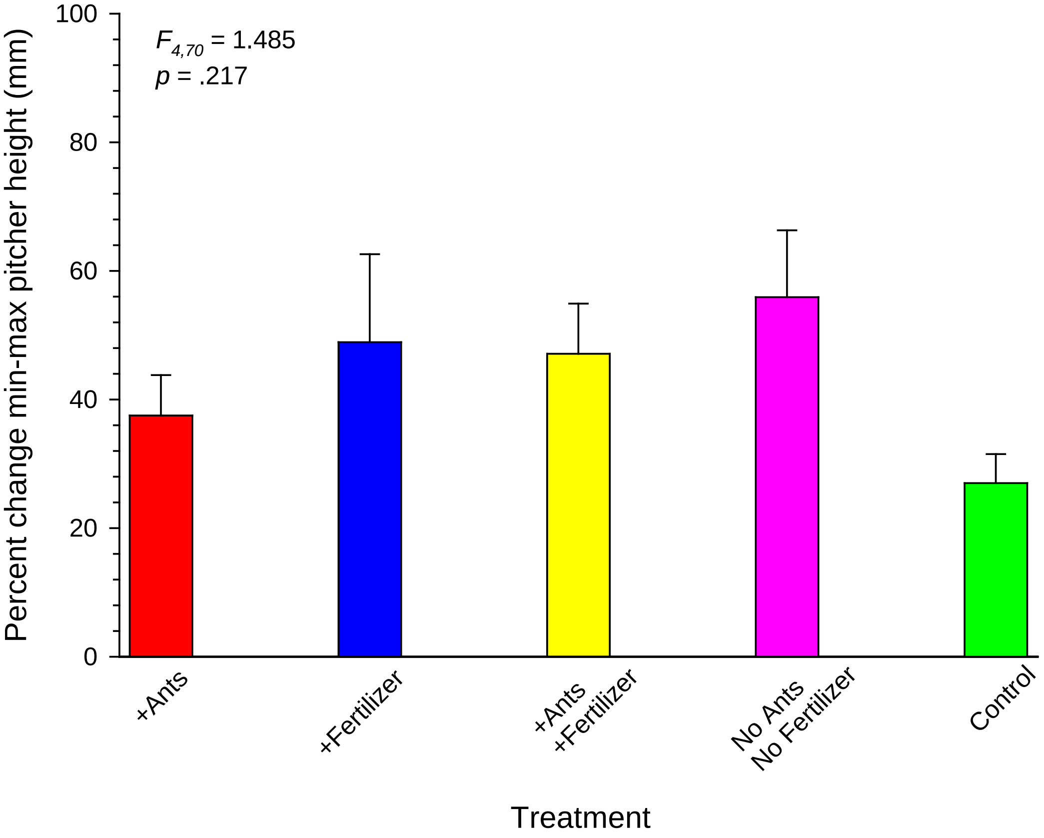

Figure 10: Percent change between the minimum and maximum pitcher height (mm).

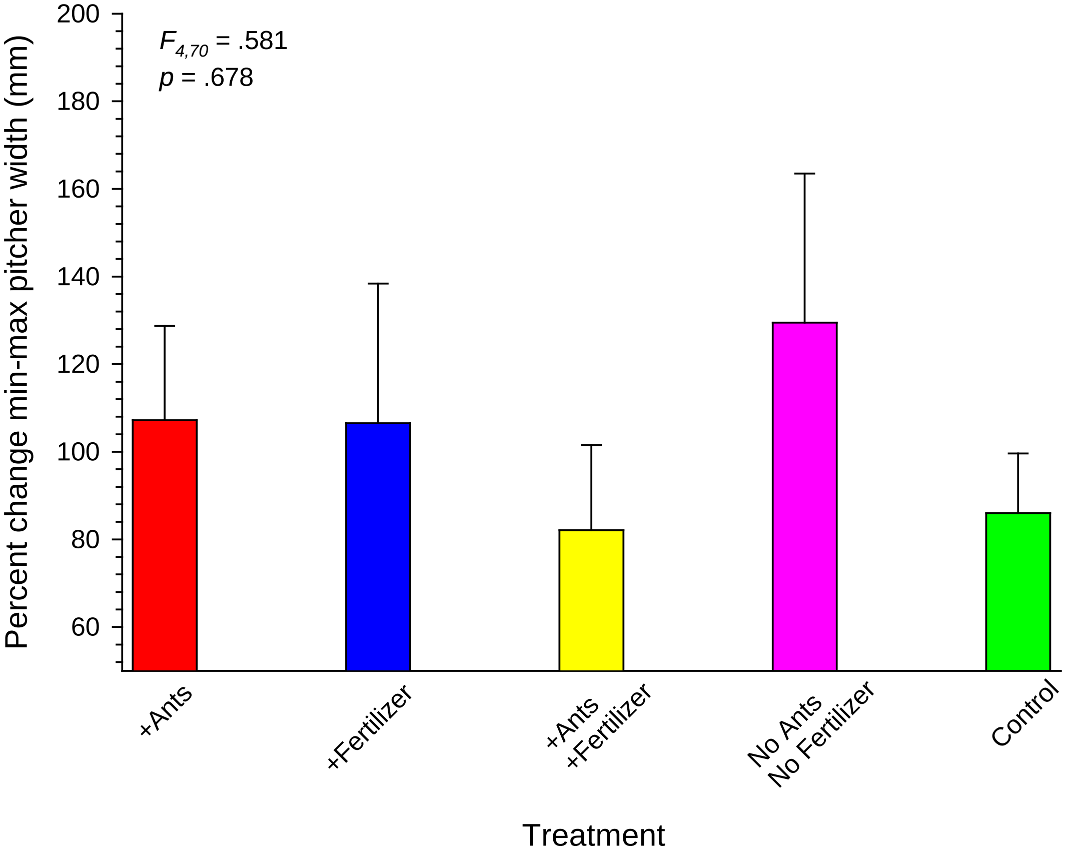

Figure 11: Percent change between the minimum and maximum pitcher width (mm).

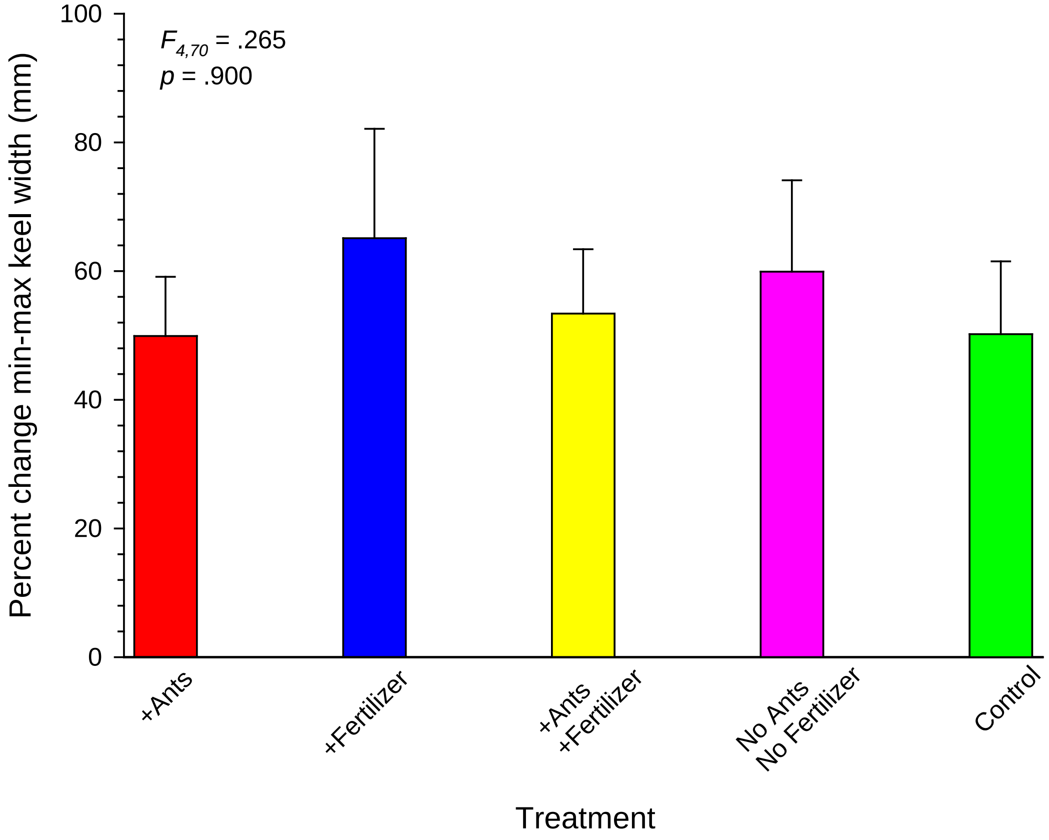

Figure 12: Percent change between the minimum and maximum keel width (mm).

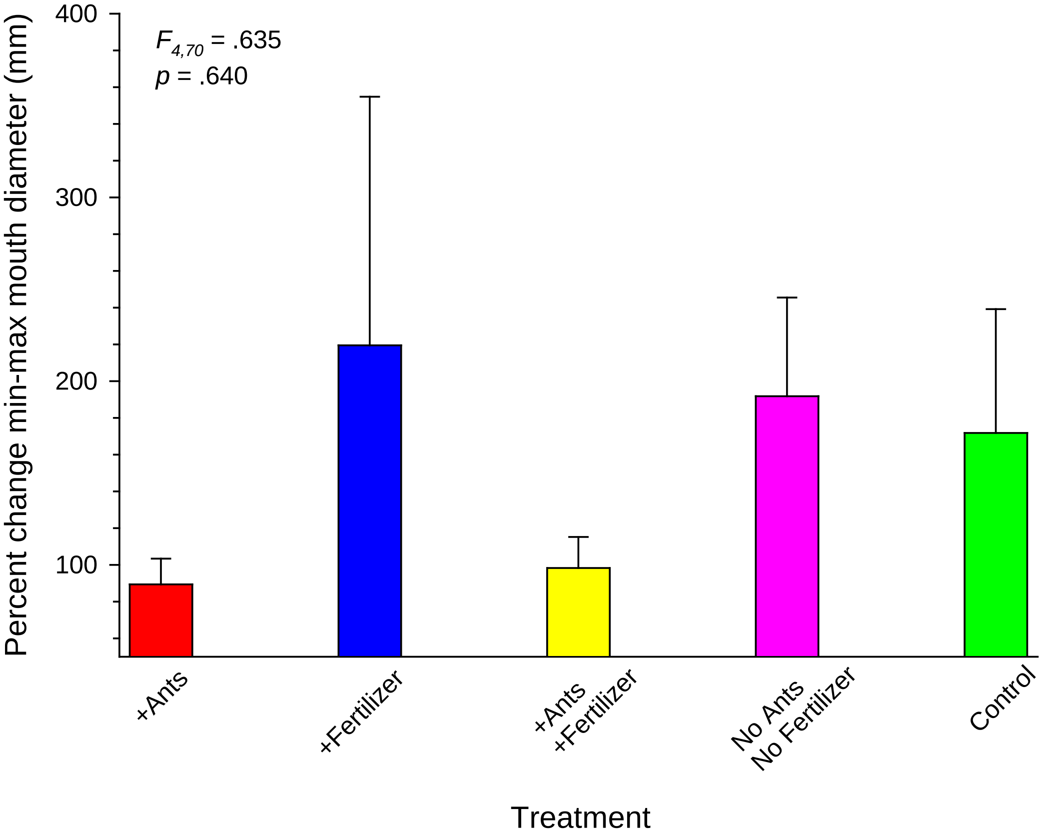

Figure 13: Percent change between the minimum and maximum mouth diameter (mm).

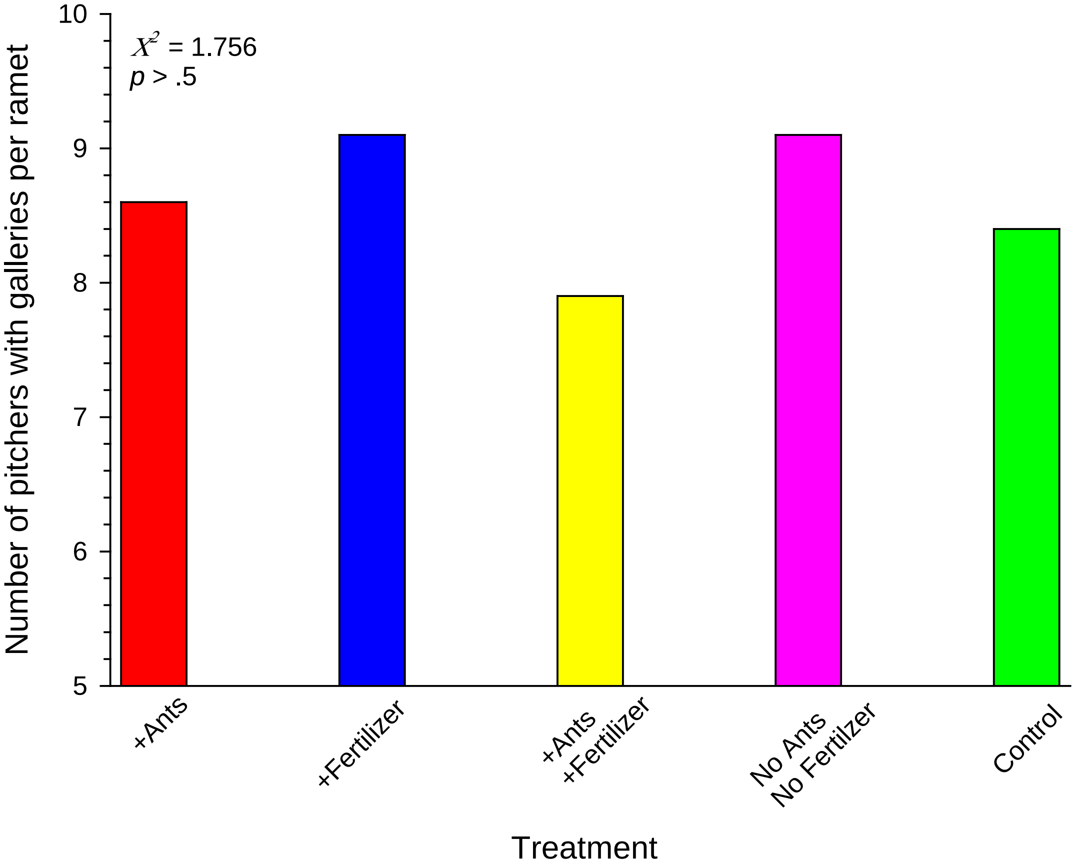

Figure 14: Number of pitchers with *E. semicrocea* galleries per ramet.

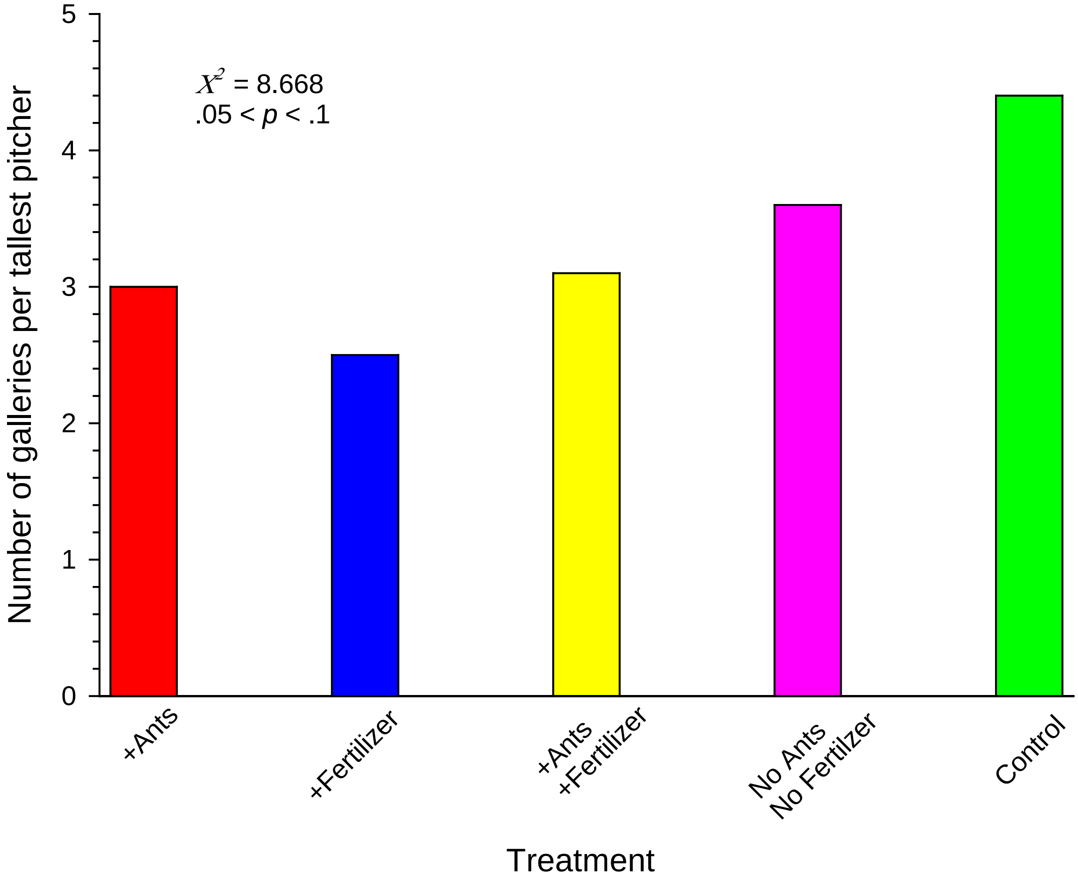

Figure 15: Number of *E. semicrocea* galleries per tallest pitcher per ramet.

Figure 16: *Solenopsis invicta* patrolling pitcher and flower. Also note *S. invicta* mound built at the base of the *S. minor* ramet.

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CURRICULUM VITAE

Education

University of North Florida, Jacksonville, FL Aug 2010-Dec 2013

M.S. Biology (Ecology)
Thesis: Nutrient availability affects flowering rate but has limited influence on morphology of the hooded pitcher plant, *Sarracenia minor.*
Major Professors: Dr. Anthony M. Rossi and Dr. Daniel C. Moon

University of New Mexico, Albuquerque, NM May 2007 (3.0 GPA)

B.S. Biology (Conservation)
Environmental Science Minor

University of San Francisco de Quito, Ecuador Aug-Dec 2004

Intensive study abroad conservation program through the
Galapagos Academic Institute for the Arts and Sciences
Independent research project: Distribution of endemic and exotic gecko species in urban environments.

Biology Experience

University of North Florida – Environmental Center April 2013 – Present
Ecologist Jacksonville, FL

- Campus Natural Assets Inventory
- Research and management of the Sawmill Slough Preserve
- Digital archiving for Sawmill Slough Preserve interactive map

Tree Hill Nature Center Sept 2012 – April 2013
Assistant Naturalist Jacksonville, FL

- Vertebrate and insect education programs
- Leading Educator of Natural Sciences for school programs
- Animal-care and grounds maintenance

Pueblo of Santa Ana – Department of Natural Resources May 2007 – Aug 2010
Biology Technician Santa Ana Pueblo, NM

- Surveys for yellow-billed cuckoo, gray vireo, endangered southwestern willow flycatcher
- Trapping and radio telemetry for wild turkey and pronghorn antelope reintroduction programs
- Fish community sampling focused on the endangered Rio Grande silvery minnow
- Vegetation measurement in riparian and upland ecosystems using belt transects and quadrats
- Herpetofauna, small mammal, and surface arthropod trapping
- Restoration work including exotic plant control

University of Puerto Rico – El Verde Field Station Sept – Dec 2006
Luquillo Forest Dynamics Plot Intern Luquillo, PR

- Collected tree census data: identification, size measurements and health characteristics
- Independent project: gathered vegetation data to correlate with point-counts

<u>University of New Mexico – The Cripps Laboratory</u> May 2005 – Aug 2006
Laboratory Assistant Albuquerque, NM

- Collected and maintained *Drosophila melanogaster* stocks and stained embryos
- Analyzed muscle development and heart defects of selected embryos

Teaching Experience

<u>University of North Florida – Department of Biology</u> Aug 2010 – May 2013
Graduate Teaching Assistant Jacksonville, FL

- General Biology I lab, Principle of Biology lab, Ichthyology lab
- Guest lecturer for Principles of Biology

Presentations

- Lemmons, J., D.C. Moon and A.M. Rossi. 2012. Effects of prey and fertilizer addition on the hooded pitcher plant, *Sarracenia minor* (poster). *UNF Biology, Chemistry, and Physics Student Poster Session*. Jacksonville, FL
- Lemmons, J., D.C. Moon and A.M. Rossi. 2012. Effects of prey and fertilizer addition on the hooded pitcher plant, *Sarracenia minor* (poster). *Southeastern Estuarine Research Society Semiannual Conference*. Jacksonville, FL.
- Lemmons, J., D.C. Moon and A.M. Rossi. 2013. Nutrient availability affects flowering rate but has limited influence on morphology of the hooded pitcher plant, *Sarracenia minor* (poster). *Florida Society of Environmental Analysts Fall Meeting*. Palm Beach, FL.
- Lemmons, J., A. Bauernfeind and C. Hubbuch. 2013. Sawmill Slough Preserve, University of North Florida (poster). *Florida Society of Environmental Analysts Fall Meeting*. Palm Beach, FL.

Memberships

- Ecological Society of America (ESA)
- Entomological Society of America (ESA)
- Florida Society of Environmental Analysts (FSEA)
- Florida Marine Science Educators Association (FMSEA)

License and Certification

- Florida Fish and Wildlife Conservation Commission (FWC)/Florida Marine Science Educators Association (FMSEA) Aquatic Species Collecting Certificate
- Listed on the Pueblo of Santa Ana's southwestern willow flycatcher endangered species permit
- Wildland firefighter red card (type 1-squad boss, type 2, incident commander type 5)
- PADI open water scuba
- CPR and first aid

Volunteer Experience

- Wolf-tracking expedition, UNF Wilderness Alliance, NM	2007
- Room monitor, National Association of Environmental Professionals, NM	2006
- Kangaroo rat research project, Sevilleta Wildlife Refuge, NM	2005
- Induced meandering project, Hubble Trading Post, AZ	2004

Skills and Equipment Knowledge

- Conversational Spanish
- GPS Navigation and back-country mapping
- Experimental design, data collection and analysis
- Species identification and sampling methods for Florida and New Mexico flora/fauna
- Water quality analysis using YSI meter
- Marsh McBirney Flo-mate and top setting rod for water velocity
- Computer skills: SPSS, Microsoft Office, Photoshop
- GIS mapping software and database management programs
- River substrate measurements, well-sounding, fencing, welding, solid waste composting
- Comfortable and self-sufficient in remote field situations for extended periods of time