

THE EFFECTS OF LIGHT AVAILABILITY, PREY CAPTURE, AND THEIR INTERACTION ON PITCHER
PLANT MORPHOLOGY

by

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INTRODUCTION

Bog habitats support a unique assemblage of organisms (Renou-Wilson et al. 2019), but they are being decimated in the United States due to human encroachment, land-use conversion (Dahl and Pywell 1989), and human abatement of fires (Johnson and Hale 2002). This is especially true for carnivorous plant bogs (Folkerts 1977). According to the New England Carnivorous Plant Society, up to 95% of carnivorous plant habitat has been lost in the United States, and various carnivorous plant species are being placed on the endangered species list (Furches et al. 2013). Therefore, it is increasingly important that we understand the species interactions and environmental factors that influence the survival and conservation of these unique organisms.

The nature of carnivorous plants and their evolved specialization of prey capture have been studied since Darwin (1875). The soils of carnivorous plant bogs are typically deficient in nitrogen, phosphorus, and/or potassium (Ellison 2006). Prey capture allows carnivorous plants to acquire additional nutrients and survive under these conditions. However, carnivorous adaptations come at a cost (Karagatzides and Ellison 2009) and reduce photosynthetic rate and photosynthetic nutrient-use efficiency (Ellison 2006). Therefore, botanical carnivory has been hypothesized to be advantageous only under conditions of high light intensity and abundant water (Givnish 1984).

Most carnivorous plants are small in stature. Therefore, in order for high light conditions to persist in these environments, disturbances are typically required to remove competing vegetation. As a result, many carnivorous plants in the southeastern United

States are dependent on periodic fire disturbances (Schnell 1976). If left undisturbed, woody vegetation can invade carnivorous plant bogs and become major competitors for light. Fires reduce the presence of invading competitive species (Brewer 2006) and can return beneficial nutrients to the soil (Weiss 1980).

If a fire has not occurred recently and resource availability (light) is being reduced, then carnivorous plants will respond morphologically (Barker and Williamson 1988). Phenotypic plasticity allows plants to alter their morphology in response to resource availability (Via and Lande 1985). Under conditions of low light or high soil nutrients, carnivorous plants may invest less in carnivorous machinery (Brewer 2003; Gotelli and Ellison 2002) and produce non-carnivorous leaves. Nutrient acquisition rates from prey capture can also influence plant morphology (Farnsworth and Ellison 2008). Prey capture rates and competition with neighboring plants have been shown to impact carnivorous plant morphology (Brewer 2003). The impact of reduced light availability via shade structures, which allows for below ground competition between carnivorous and heterospecific non-carnivorous neighbors, and its interaction with prey capture rates is yet to be studied.

The goal of this study was to examine the effects of light availability, prey capture, and their interaction on morphology of the carnivorous plant, *Sarracenia alata*. The pale pitcher plant, *S. alata*, has pitcher-shaped leaves that function for both photosynthesis and prey capture. Pitcher morphology is affected by resource availability. In low light environments pitchers grow taller with a smaller opening to maximize light capture, whereas in high light conditions pitchers are shorter with wider openings to maximize prey

capture (Brewer 1999). The morphology of the pitcher plant is also affected by rates of prey capture (Farnsworth and Ellison 2008), which in turn can be affected by both natural prey availability and by the pitcher moth, *Exyra semicrocea*. Larvae of this noctuid moth can reduce or prevent pitcher prey capture by spinning a web that obstructs the pitcher openings (Carmickle and Horner 2019). The abatement of prey capture results in a loss of nutrient uptake and can negatively impact plant growth and fitness.

We predicted that pitcher plants that experience low light availability and/or loss of prey capture would exhibit a morphology reflective of the associated resource limitation. We hypothesized that under conditions of low light availability, pitcher plants would have greater height-to-diameter ratios (grow taller with smaller diameters) to maximize light capture. Under conditions of reduced prey capture, we hypothesized that pitcher plants would exhibit reduced growth rates (fewer pitchers and lower sum of pitcher heights). We hypothesized that the interaction of low light and loss of prey capture would result in pitchers with a greater height-to-diameter ratio as well as reduced growth due to reduced resource availability.

METHODS

Study Organism

Sarracenia alata, the pale pitcher plant, is a rhizomatous carnivorous plant that is native to the southeastern United States from Alabama to eastern Texas (Schnell 2002). It produces a single flower at the beginning of the growing season and subsequently produces funnel-shaped leaves called pitchers that are specialized for prey capture (Horner 2014). A rib or keel extends along one side of the pitcher. Several *Sarracenia* species (e.g., *S. purpurea*; (Gotelli and Ellison 2002) produce leaf-like phyllodia. The pale pitcher plant does not produce phyllodia, but under certain conditions, they produce pseudo-phyllodia, which are blade-like pitchers with small (less than 2 mm diameter), non-functional openings and widened keels. The pitchers open after they reach their maximum height (Horner et al. 2012). An extension of leaf tissue referred to as the hood covers but does not occlude the opening. Surrounding the opening is a slippery lip called the peristome. Nectar and volatiles attract prey to the peristome, where they slip and fall into the pitcher (Juniper et al. 1989; Horner et al. 2018). The lower portion of the pitcher interior is lined with downward pointing hairs that prevent escape of the prey, and the bottom contains enzymes that digest the prey.

Field and Laboratory Methods

The study employed a two-factor, cross-classified design, with shading (two levels, shaded and unshaded) and prey capture (two levels, fed and unfed) as factors. Eighty plants were chosen and haphazardly assigned to one of four treatments (20 plants in each): (1) unshaded and fed (control); (2) shaded and fed; (3) unshaded and unfed; and (4) shaded and unfed. The treatments were applied 14-April-2019. Plants in treatments receiving shade were covered by a 50% light reduction shade cloth cover suspended by an 80cm x 80cm x 80cm cube constructed with 1.9-cm polyvinylchloride (PVC) pipe. The shade cloth extended 30 cm down the sides of the PVC structure. Plants in the unshaded treatments had unmanipulated light availability. Individuals in the treatments receiving feeding were surrounded at the base by herbivore-exclusion rings that were 10.2-cm-tall, 10.2-cm-diameter PVC rings. The rings were coated with a sticky insect trap (Tanglefoot) to prevent *Exyra* larvae from crawling up the pitchers (Carmickle and Horner 2019). The pitcher openings were plugged with cotton to prevent *Exyra* adults from ovipositing. Loss of prey capture caused by plugging the opening was compensated for by supplementing dried, ground mealworms. The quantity supplied was based on the estimated seasonal capture rates of pitchers of comparable size (Carmickle and Horner 2019). Pitchers with an opening less than 1 cm in diameter were provided with 0.104 ± 0.033 g; pitchers with a 1–2 cm diameter opening were provided with 0.210 ± 0.014 g; and pitchers with an opening greater than 2 cm diameter were provided with 0.442 ± 0.018 g. Plants in the unfed treatments were also plugged but were not fed the supplemental mealworms.

There was a prescribed burn at the study site on 18-February-2019. This burn removed much of the competing vegetation. We noticed that as the season progressed, non-carnivorous competing vegetation began to return and eventually dominate. This reduced light availability to pitchers in all treatments as indicated by measurements of photosynthetically active radiation (PAR). Because of this unexpectedly quick regeneration of competing vegetation, we decided to separate the season into three periods: the Early Season (14-April-2019 to 29-May-2019,) which examined the effects of the field manipulation experiment; a transitional phase; and the Late Season (31-July-2019 to 20-October-2019), which examined the effects of the natural experiment caused by rapid regrowth of vegetation.

We visited the site weekly from April until June, every 10 days from June through July, then every two weeks until the end of growing season in October. As new pitchers opened, they were tagged by wire clips and pitchers in the appropriate treatments were fed. Two visits after being tagged, the height (ground to peristome) and diameter of the opening of each pitcher were measured. Keel width was measured once in Early Season and during every visit in Late Season. We recorded PAR at ground level, PAR at pitcher height (average 40 cm from ground), and temperature monthly at each study genet.

At the end of the season, we collected 70 0.20-cm² discs of pitcher and keel tissue from haphazardly selected study pitchers from all treatments to determine the specific leaf mass of pitchers and keels. We also collected 69 whole pitchers (maximum 2 per genet) from plants approximately evenly distributed among all treatments. The punches were placed in airtight plastic vials and whole pitchers were transported in plastic Ziploc bags

with a tissue soaked in bog water to maintain moisture. The wet mass of discs and whole pitchers was measured the following day. Both discs and pitchers were then dried in an oven at 60 degrees Celsius for 72 hours, after which their dry mass was recorded. Specific leaf mass (mass/unit area) was determined for pitchers and keels for each treatment by dividing the dry mass of discs by the area (0.20 cm²)

Leaf Mass

The surface area for each of the 69 collected pitchers was estimated by calculating the area of a cone ($A = \pi * \text{radius}(\text{radius} + \sqrt{(\text{height}^2 + \text{radius}^2)})$) for pitcher area and the area of a cylinder ($A = 2 * \pi * \text{radius} * \text{height}$) for the rib of pseudo-phyllodia. The surface area of keels was estimated as the area of half an ellipse ($A = (\pi * (\text{height}/2) * \text{radius})/2$). Pitcher mass was estimated by multiplying the calculated area of each pitcher and keel by the specific leaf mass for the tissue from that treatment. The estimated masses were regressed against the actual dry masses of the corresponding collected pitcher. The regression yielded correction formulae that were applied to all pitchers; pitcher mass = $1.766x^{1.0706}$ ($R^2 = 0.89$; x = estimated pitcher mass), pseudo-phyllodia mass = $1.7614x^{1.3809}$ ($R^2 = 0.65$; x = estimated pitcher mass). A single regression for each pitcher and pseudo-phyllodia was used as there was no significant difference between the specific leaf masses of the different treatments. The mass of each pitcher measured throughout the season was then estimated by calculating the surface area multiplied by specific leaf mass, then corrected with the regression equation. Because keel measurements were only taken once in the Early Season and because keel width was

minimal in the Early Season, Early Season pitcher mass was estimated by using the area of the cone; keel mass was not factored into estimated pitcher mass for pitchers in the Early Season.

Statistical analysis

Height-to-diameter ratio was calculated by $\log(\text{height/diameter})$ (Brewer 2019), and height-to-keel ratio was calculated by $\log(\text{height/keel})$. The mean pitcher heights per genet, mean diameters per genet, mean height-to-diameter ratios per genet, mean keel width per genet, mean height-to-keel ratios per genet, number of pitchers per genet, summed masses per genet, and sum of pitcher heights per genet were analyzed by separate two-factor analyses of variance (ANOVA), with shade and feeding as the factors with two levels each. Mean seasonal (Early versus Late) differences for diameters, keel width, and ground PAR were compared using a Student's t-test assuming equal variance. Measurements of PAR were log transformed to improve heteroscedasticity. Temperature and log-transformed PAR were also analyzed by a two-factor ANOVA with shade and feeding as factors (each with two levels) and time of day as a covariate. Statistical significance was determined at $\alpha = 0.05$ for all tests. Analyses were performed in Minitab 18.

RESULTS

Field Manipulation: Early Season (14-April-2019 to 29-May-2019)

The shade structures reduced PAR in the shaded treatments at both ground level ($F_{0.05(2),3,76} = 7.25$, $p = 0.009$; Figure 1) and at pitcher height ($F_{0.05(2),3,76} = 25.55$, $p < 0.001$).

The shade structures had no significant effect on temperature ($p = 0.310$).

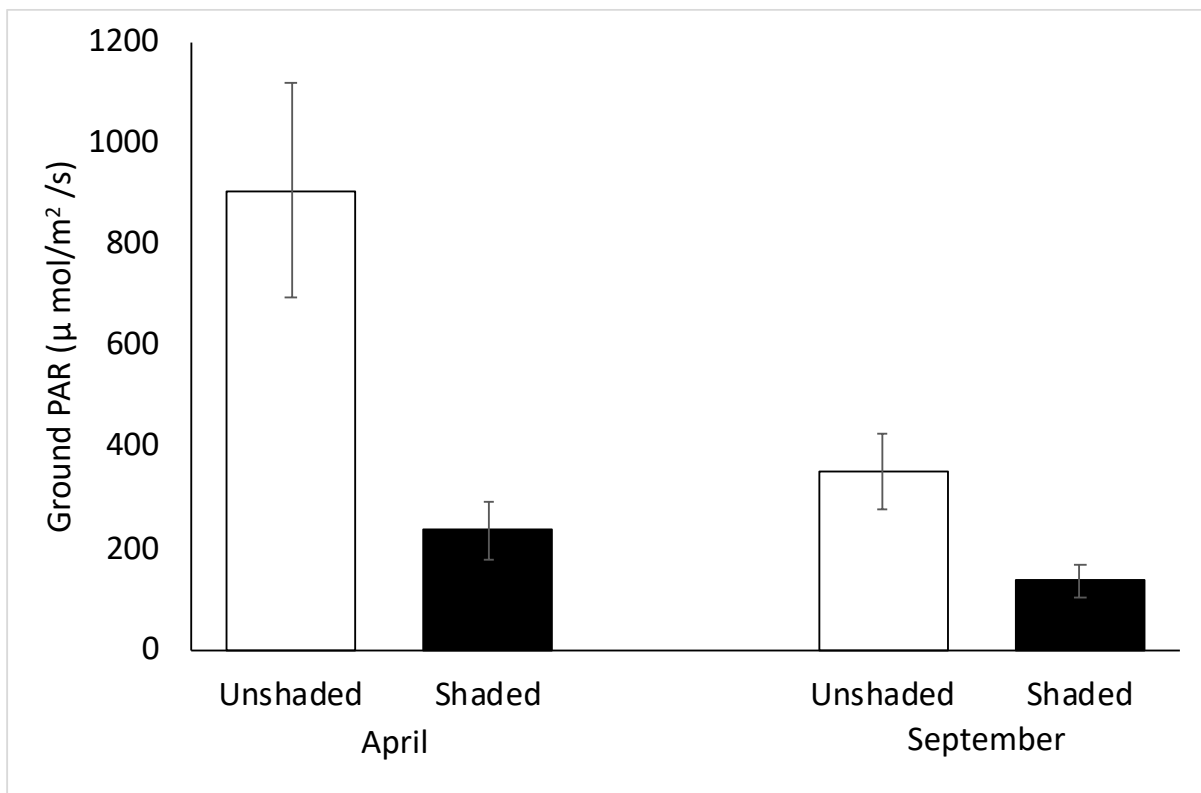


Figure 1 Ground height PAR ($\mu\text{mol}/\text{m}^2/\text{s}$) per genet for unshaded and shaded treatments for April (Early Season) and September (Late Season). Error bars are ± 2 SE.

The shade treatment affected pitcher morphology. Average pitcher diameter per genet was significantly smaller in plants in the shaded treatments (Table 1; Figure 2). There

was no significant impact of treatments on average height-to-diameter ratio per genet (Table 2).

Table 1 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on average pitcher diameter per genet for Early and Late Seasons.

	Source	SS	df	F	p
Early Season	Feeding (F)	0.079	1	0.33	0.566
	Shading (S)	1.079	1	4.53	0.037
	Interaction (FxS)	0.100	1	0.42	0.520
	Error	18.094	76		
Late Season	Feeding (F)	0.238	1	0.62	0.434
	Shading (S)	0.039	1	0.10	0.750
	Interaction (FxS)	1.171	1	3.06	0.085
	Error	23.753	62		

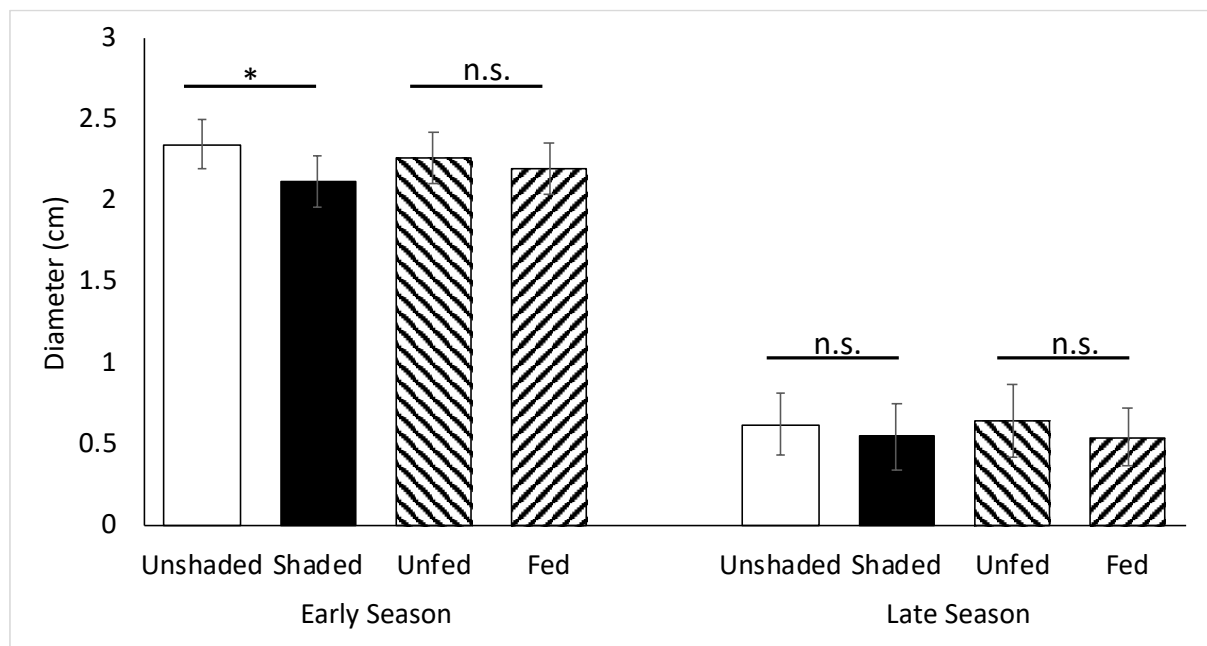


Figure 2 Effects of feeding and shading on average diameter (cm) of pitchers per genet for Early and Late Seasons. Error bars are ± 2 SE. (n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Table 2 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on average height-to-diameter ratio per genet for Early and Late Seasons.

	Source	SS	df	F	p
Early Season	Feeding (F)	0.011	1	1.59	0.211
	Shading (S)	0.022	1	3.20	0.078
	Interaction (FxS)	0.001	1	0.21	0.652
	Error	0.526	76		
Late Season	Feeding (F)	0.069	1	0.36	0.548
	Shading (S)	0.191	1	1.01	0.320
	Interaction (FxS)	0.810	1	4.26	0.043
	Error	11.790	62		

The average pitcher height per genet was not significantly affected by the feeding treatments ($p = 0.161$). Unfed plants had fewer pitchers (Table 3; Figure 3) and a lower sum of pitcher heights (Table 4; Figure 4), but these differences were not significant. There were significant effects of shading and the interaction between shading and feeding on estimated leaf mass per genet (Table 5; Figure 5).

Table 3 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on average number of pitchers per genet for Early and Late Seasons.

	Source	SS	df	F	p
Early Season	Feeding (F)	15.312	1	3.62	0.061
	Shading (S)	1.103	1	0.24	0.626
	Interaction (FxS)	15.312	1	3.62	0.061
	Error	312.850	76		
Late Season	Feeding (F)	40.610	1	5.64	0.020
	Shading (S)	52.810	1	7.33	0.008
	Interaction (FxS)	25.310	1	3.51	0.065
	Error	547.650	76		

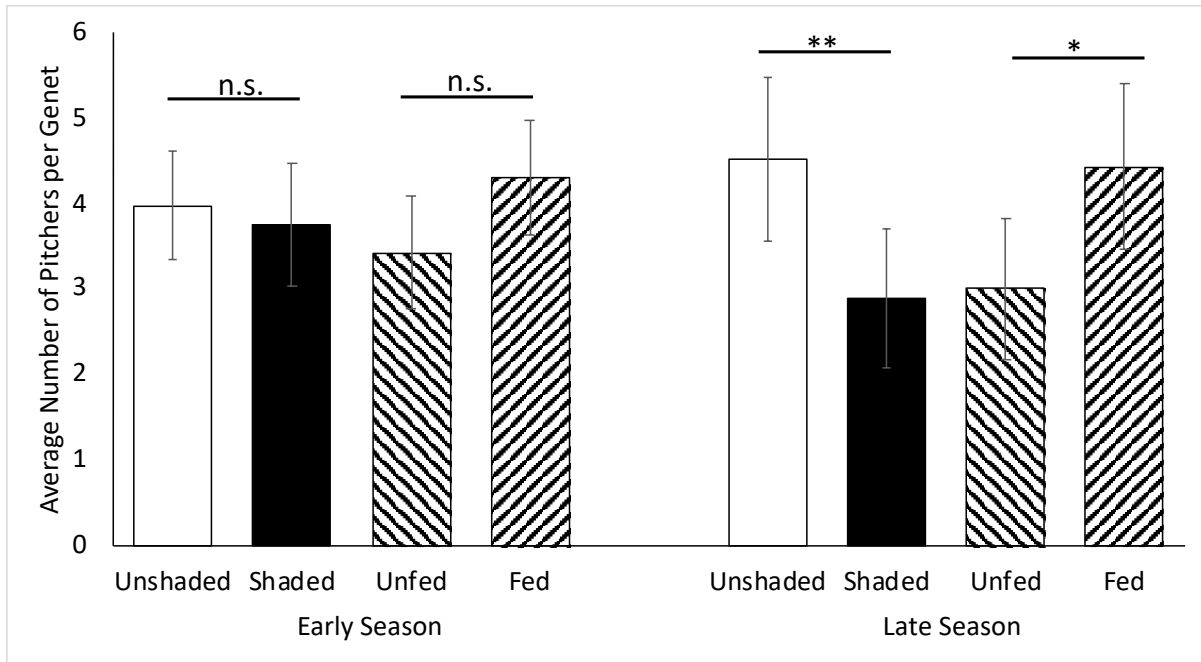


Figure 3 Effects of feeding and shading on average number of pitchers per genet for Early and Late Seasons. Error bars are ± 2 SE. (n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Table 4 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on average sum of pitcher heights per genet for Early and Late Seasons.

	Source	SS	df	F	p
Early Season	Feeding (F)	23,120	1	3.07	0.084
	Shading (S)	5,763	1	0.76	0.385
	Interaction (F \times S)	16,832	1	2.23	0.139
	Error	573,024	76		
Late Season	Feeding (F)	40,888	1	4.44	0.038
	Shading (S)	30,521	1	3.32	0.072
	Interaction (F \times S)	19,877	1	2.16	0.146
	Error	699,289	76		

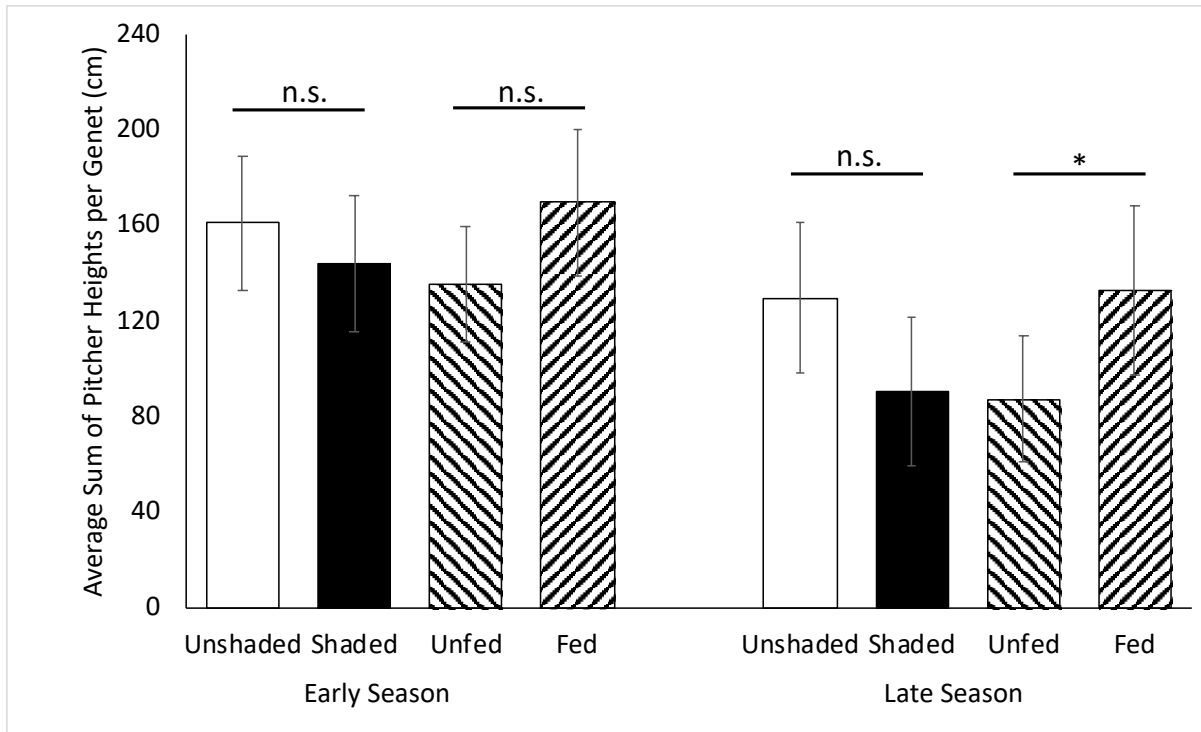


Figure 4 Effects of feeding and shading on average sum of pitcher heights (cm) per genet for Early and Late Seasons. Error bars are ± 2 SE. (n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Table 5 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on sum of estimated leaf mass per genet for Early and Late Seasons.

	Source	SS	df	F	p
Early Season	Feeding (F)	0.45	1	0.15	0.701
	Shading (S)	15.80	1	5.24	0.025
	Interaction (F \times S)	33.17	1	10.99	0.001
	Error	226.30	76		
Late Season	Feeding (F)	10.63	1	2.85	0.096
	Shading (S)	18.67	1	5.00	0.028
	Interaction (F \times S)	19.67	1	5.27	0.024
	Error	283.83	76		

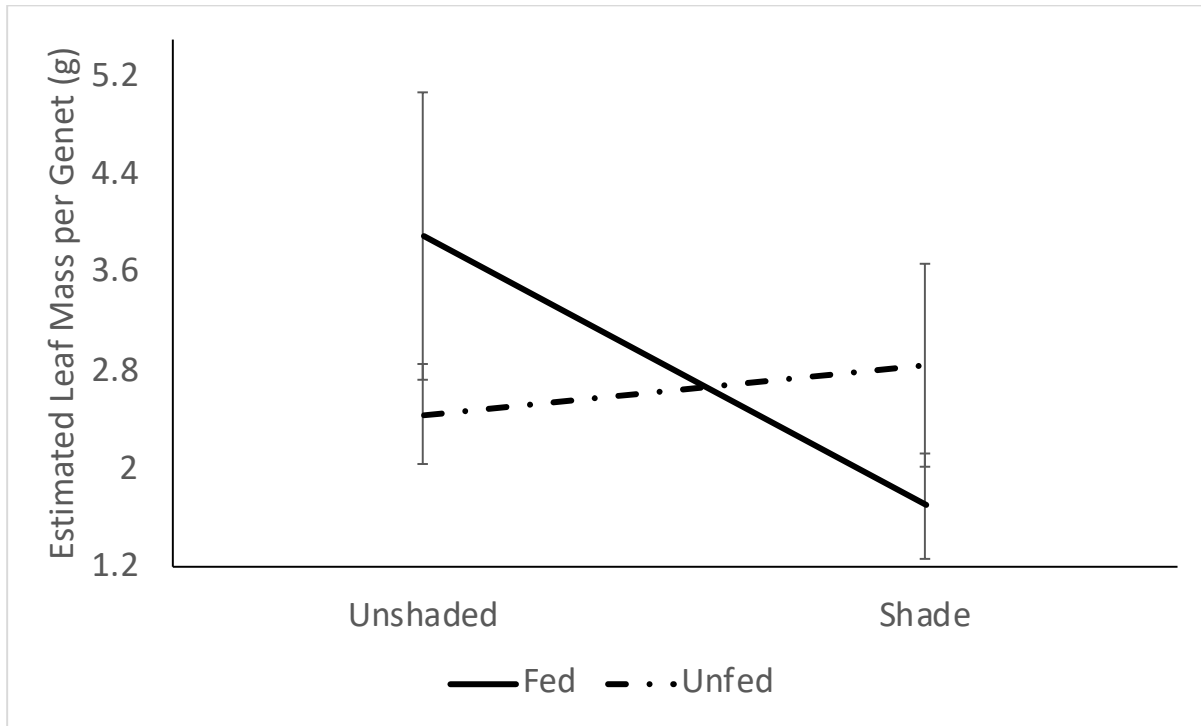


Figure 5 Interaction plot of the effects of feeding, shading, and their interaction on sum of estimated leaf mass (g) per genet for Early Season. Error bars are ± 2 SE.

Natural Experiment: Late Season (31-July-2019 to 20-October-2019)

Late in the growing season, shade structures continued to significantly reduce PAR at ground height ($F_{0.05(2),3,76} = 54.68$, $p < 0.001$) and pitcher height ($F_{0.05(2),3,76} = 144.47$, $p < 0.001$) compared to unshaded plants, but PAR decreased across all treatments (Figure 1). Mean ground PAR across all treatments for the Late Season ($247.99 \pm 66.78 \mu\text{mol}/\text{m}^2/\text{s}$, $n = 80$) was significantly lower ($t_{0.05(2)156} = 4.66$, $p < 0.001$) than that in the Early Season ($582 \pm 23.74 \mu\text{mol}/\text{m}^2/\text{s}$, $n = 78$).

The average diameter per genet across all treatments in the Late Season ($0.59 \pm 0.08\text{cm}$, $n = 66$) was significantly smaller ($t_{0.05(2),144} = -17.77$, $p < 0.001$) than that in the Early Season ($2.23 \pm 0.06\text{cm}$, $n = 80$). In contrast to results in the Early Season, there was no significant effect of shading on the average diameter per genet in the Late Season (Table 1; Figure 2). However, there was a significant interaction effect on height-to-diameter ratio per genet (Table 2; Figure 6). Fed plants in the shade had a higher height-to-diameter ratio than those in full sun. Unfed plants in full sun had a greater height-to-diameter ratio than those in shade.

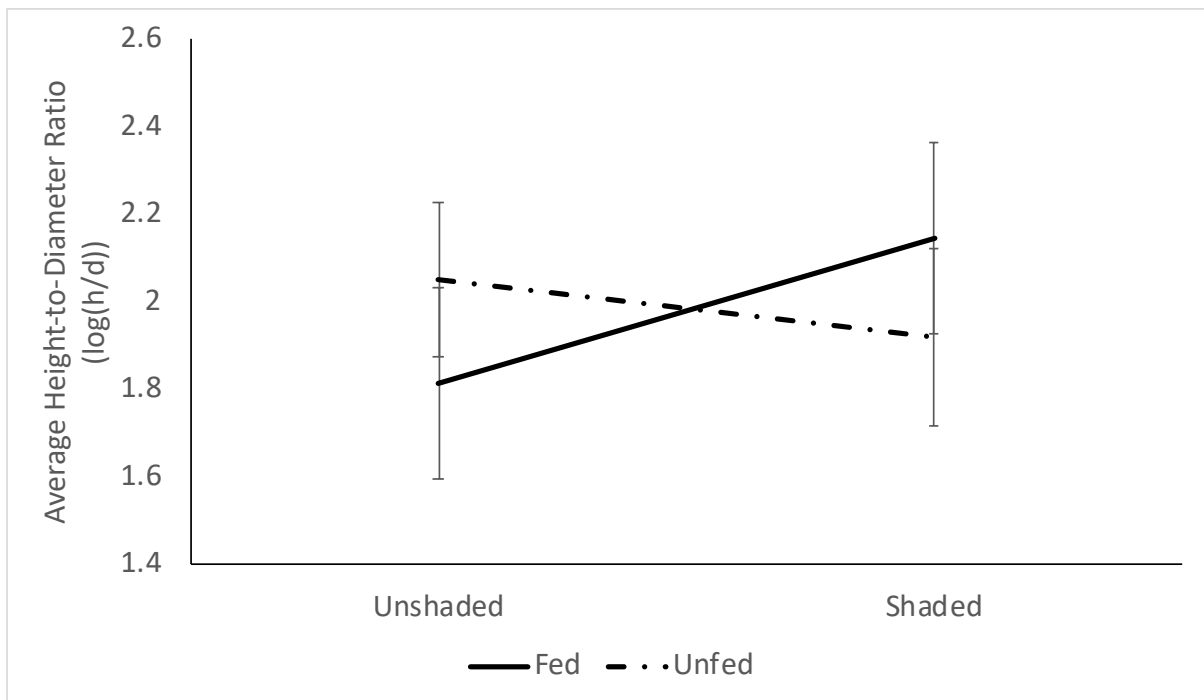


Figure 6 Interaction plot of the effects of feeding, shading, and their interaction on average height-to-diameter ratio ($\log(h/d)$) per genet for Late Season. Error bars are ± 2 SE.

Treatments affected plant growth in the Late Season. There were significantly fewer pitchers produced per genet in the unfed and shaded treatments (Table 3; Figure 3). The

sum of pitcher heights per genet was significantly lower in the unfed treatments (Table 4; Figure 4). There was a significant interaction effect on estimated leaf mass per genet (Table 5; Figure 7). The estimated mass per genet was not significantly affected by shading in unfed plants, but shading reduced mass of fed plants.

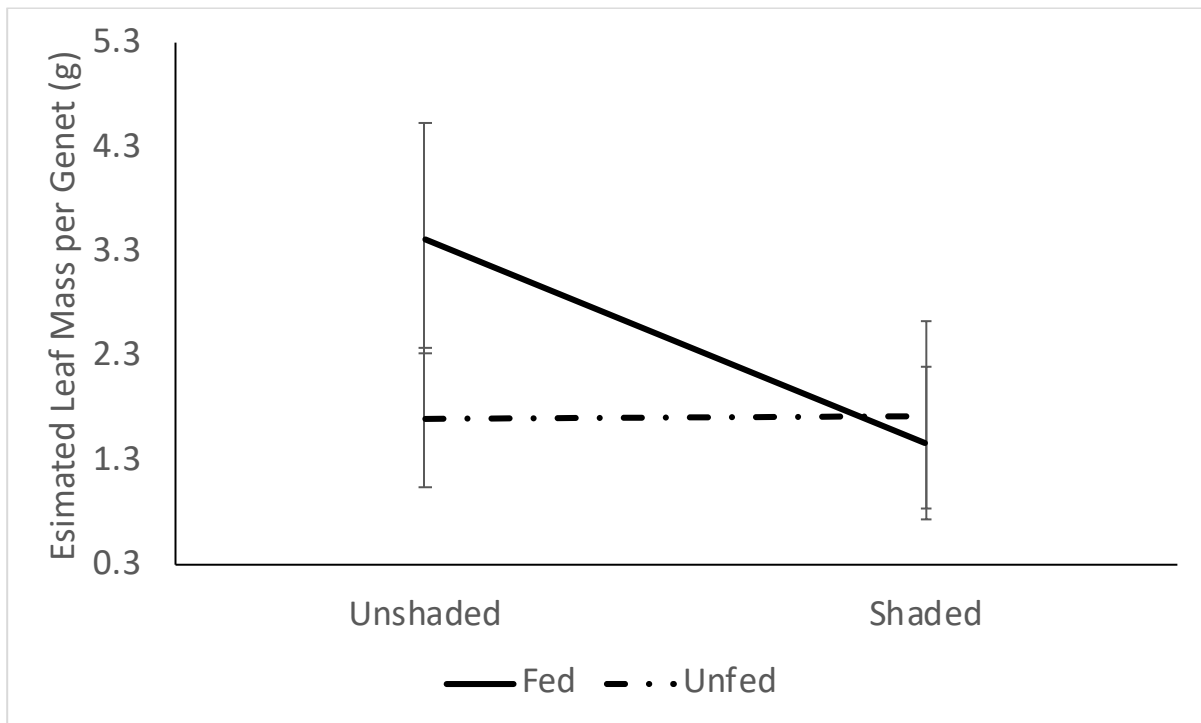


Figure 7 Interaction plot of the effects of feeding, shading, and their interaction on sum of estimated leaf mass (g) per genet for Late Season. Error bars are ± 2 SE.

Pitcher keels across all treatments in the late season (9.88 ± 0.35 mm, $n = 71$) were significantly wider ($t_{0.05(2),115} = -12.53$, $p < 0.001$) than those in the Early Season (4.19 ± 0.21 mm, $n = 46$). The ratio of height-to-keel width significantly changed over the growing season; pitchers from the Late Season had wider keels (thus a smaller ratio) than those in the Early Season (Table 6; Figure 8).

Table 6 Summary of analysis of variance (ANOVA) of the effects of feeding, shading, and their interaction on height-to-keel ratio nested within date.

Source	SS	<i>df</i>	<i>F</i>	<i>p</i>
Feeding (F)	0.07	1	3.27	0.073
Shading (S)	0.02	1	0.92	0.339
Interaction (F×S)	0.01	1	0.05	0.827
Date (F,S)	4.13	4	50.43	0.001
Error	2.19	107		

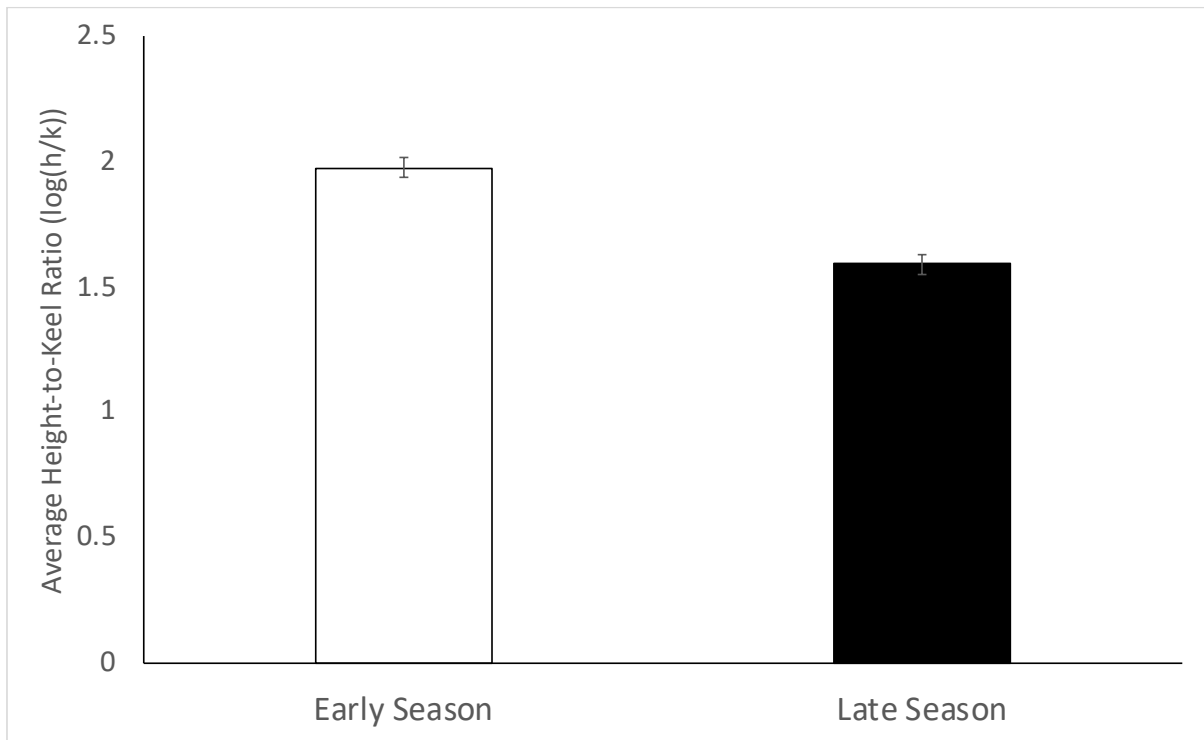


Figure 8 Average height-to-keel ratio (log(height/keel)) for all genets across all treatments for Early and Late Seasons. Error bars are ± 2 SE.

DISCUSSION

Early Season: field manipulation

The prediction for the Early Season “field manipulation” was that pitcher plants that experienced low light availability and/or loss of prey capture will exhibit a morphology reflective of the associated resource limitations. We hypothesized that under conditions of low light availability, pitcher plants would have greater height-to-diameter ratios (grow taller with smaller diameters) to maximize light capture. Under conditions of reduced prey capture, we hypothesized that pitcher plants would exhibit reduced growth rates (fewer pitchers and lower sum of pitcher heights). We hypothesized that the interaction of low light and loss of prey capture would result in pitchers with a greater height-to-diameter ratio but would also exhibit reduced growth due to lessened resource availability. These phenotypic responses occurred in ecological time.

Shaded plants produced pitchers that had smaller diameters. This could be interpreted as a shift towards a photosynthetic morphology, maximizing light interception by increasing surface area at the expense of prey capture. The smaller diameter may be interpreted as a reduced dependence on prey capture in conditions of low light, as capture rates positively correlate with opening size (Heard 1998; Green and Horner 2007; Bhattarai and Horner 2009). Thus, reduced light availability led to a morphology that would maximize light interception and decrease prey capture.

Unfed plants had lower growth rates. Carnivorous machinery is an expensive investment (Karagatzides and Ellison 2009), and prey exclusion from pitchers likely reduced nutrient capture. In the Early Season, unfed plants produced fewer pitchers per genet and had lower sum of pitcher heights per genet than fed plants, although this difference was not statistically significant. We hypothesize that differences in indices of growth accrue over the season. This may explain why significant differences in growth were only observed in the Late Season, as insufficient time had elapsed for the treatments to significantly impact growth in the Early Season.

Plant growth was significantly affected by the interaction between feeding and shading. When the plant was unfed, shade did not affect estimated leaf mass. This may be because unfed plants were nutrient limited, incapable of responding to differences in light availability. Therefore, these plants produced less biomass than plants that were fed and in full sun. Shade did have a significant effect on estimated leaf mass in fed plants. Growth in fed plants was limited by light availability.

Late Season: natural experiment

Unfed pitcher plants grew less (produced fewer pitcher and had lower sum of pitcher heights) than fed plants and the interaction effects impacted plant production (estimated leaf mass) in the same manner as in the Early Season. Shaded plants grew less (produced fewer pitchers) than unshaded plants. Because overwintering and the production of the flower and first pitcher are dependent on reserves stored during the previous season

(Butler et al. 2008), the reduction in resource acquisition and growth may negatively impact survival and reproduction.

Due to the resurgence of competing vegetation and the shade it produces, light availability was reduced across all treatments in the Late Season (Figure 1). This reduction in light across all genets diminished the impact of the shade treatment and altered the morphology of all the pitchers in all treatments during the Late Season. One manifestation of this morphological shift was a reduction of average diameters across all treatments. This may explain why the significant difference in average diameters observed in shaded plants in the Early Season was not observed in the Late Season. Another morphological change that occurred in the Late Season was the significant widening of pitcher keels. The pitchers produced in the Late Season began to take on the shape of pseudo-phyllodia, with non-functional openings that ranged from never fully opening to less than 2mm in diameter. *Sarracenia alata* does not produce phyllodia (Schnell 1998; Sheridan 1991), but we found that when under conditions of low light, the plants will abandon carnivorous machinery and produce pitchers that have little to no opening and a widened keel. This morphological response had been observed in *Sarracenia purpurea* (Gotelli and Ellison 2002) when exposed to high nitrogen availability. The high levels of soil nitrogen diminished the importance of prey capture and the need for carnivorous pitchers. The abandonment of carnivorous machinery is dependent on resource availability and can occur in low light environments to maximize photosynthetic capabilities or in high nutrient environments where prey capture is no longer required.

Support for Economic Model of Carnivorous Investment

The economic model of carnivorous investment hypothesized that the evolved specialty of prey capture in carnivorous plants comes at a cost (Karagatzides and Ellison 2009) with reduced photosynthetic rate and photosynthetic nutrient-use efficiency (Ellison 2006). Thus, botanical carnivory has been hypothesized to be beneficial only under conditions of high availability of water and light (Givnish 1984). The Early Season field manipulation and the Late Season natural experiment provide support for this. In the shade treatments (or in Late Season due to competing vegetation), the pitcher plants could no longer sustain carnivorous machinery. Therefore, the plant took on a primarily photosynthetic morphology (wide keels and non-functional pitchers).

Conservation Impact

Carnivorous plant bogs are quickly being lost in the United States and some *Sarracenia* species are endangered (Furches et al. 2013). For species that are not currently endangered, they are at risk of becoming so due to shrinking habitats and fragmented populations (Folkerts 1977). The pseudo-phyllodia morphological response expressed by the pitchers to light competitors is a beneficial short-term adaptation. In the long-term, if these conditions persist over numerous seasons, this morphology can be detrimental for survival as overwintering and the production of the flower and first pitcher are dependent on reserves stored during the previous season (Butler and Ellison 2007). This loss of nutrient

acquisition can impact fitness and expedite the local extinctions of this species and similar carnivorous plants.

Natural fires typically occur every three to four years in the habitats occupied by carnivorous plants in the southeastern United States, but humans suppressed fires until recent shifts in conservation ideologies in the 1970s (Johnson and Hale 2002). Fire suppression can cause competing vegetation to replace carnivorous plants. Therefore, it is critical for landowners and public land agencies to monitor their carnivorous plants for signs of morphological change and to regularly perform prescribed burns to maintain the health of the bogs and their associated organisms. The winter burn at our bog was relatively inefficient and incomplete as some shrubs remained, and competing vegetation was able to quickly recover. This may have been due to the timing of the burn (i.e. winter burn), which is less efficient at reducing competing vegetation (Brewer 1999). Another factor that may have allowed for the quick recovery of the competing vegetation was the low intensity of the burn, as a low intensity fire does not penetrate into the bottom layer of vegetation or into the soil (Alcaniz et al 2018). The impact that competing vegetation has on pitcher morphology can be seen in ecological time in one growing season and can be used as an index for land managers to assess the health of their pitchers and similar carnivorous plants. Decreasing pitcher diameter, widening keels, or production of phyllodia/pseudo-phyllodia, depending on the *Sarracenia* species present, can be used as indicators that the pitchers are becoming light limited and a prescribed burn is required.

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ABSTRACT

THE EFFECTS OF LIGHT AVAILABILITY, PREY CAPTURE, AND THEIR INTERACTION ON PITCHER PLANT MORPHOLOGY

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Carnivorous plants inhabit nutrient-poor environments and supplement nutrient acquisition by prey capture. Carnivorous adaptations have been hypothesized to be beneficial only in environments with high light availability. We hypothesized that plant morphology would change in response to resource availability. In a field manipulation in Leon County, Texas, we examined the effects of feeding, shading, and their interaction on pitcher plant (*Sarracenia alata*) morphology. When light availability was reduced, plants produced pitchers that had smaller diameters. Unfed plants exhibited reduced growth. As the season progressed, competing vegetation began to reduce light availability to all pitchers. Plants in all treatments began to produce pitchers that were blade-like with a small, non-functional opening and a widened keel. This experiment provides support for the theoretical model that prey capture is only beneficial under conditions of high light availability. It also emphasizes the importance of periodic burns of carnivorous plant bogs to remove competing vegetation.