

THE ROLE OF ANTHOCYANIN AS AN ATTRACTANT IN *SARRACENIA*  
*LEUCOPHYLLA* RAF.

A THESIS

SUBMITTED TO THE GRADUATE SCHOOL

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE

MASTER OF SCIENCE

BY

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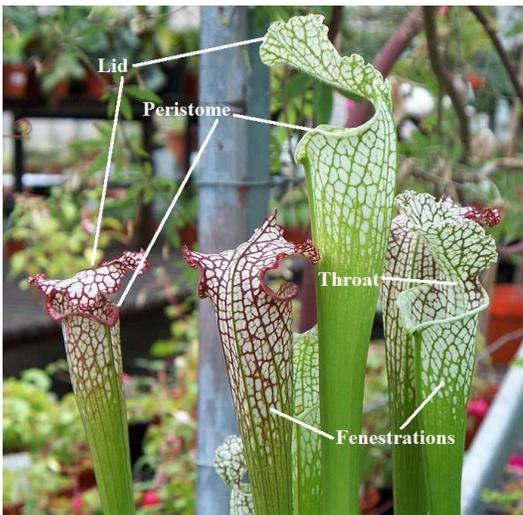
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MAY 2012

## Introduction



**Figure 1: The trumpet shaped pitchers of *Sarracenia leucophylla* illustrating phenotype coloration. Taken from: [http://www.growingmatters.co.uk/gmexotic\\_carnivores\\_pitcher-plants.htm](http://www.growingmatters.co.uk/gmexotic_carnivores_pitcher-plants.htm)**

*Sarracenia leucophylla* Raf, commonly known as the white-topped pitcher plant, is a perennial, carnivorous dicot native to the southeastern United States. Arising from clumping rhizomes, the leaves are trumpet-form in appearance and have lids with hairy undersides which point toward the pitcher opening (Figure 1) (Schnell, 2002).

These hairs presumably facilitate advancement of prey toward the pitcher mouth while making retreat challenging (Newell & Nastase, 1998). Pitcher coloring ranges from green to red and progressively changes to white fenestrations towards the pitcher top which are commonly intermixed with green and/or red venations (Figure 1). Pitcher anatomy consists of lid, peristome, throat and fenestrations (Figure 1). Flowers which occur in early spring, usually from March to May, are insect pollinated, mainly by *Bombus* species (Schnell, 1983; 2002) and readily cross pollinate within the genus.



**Figure 2: A comparison of anthocyanin-free (left) and anthocyanin present (right) pitchers.**

The evolution of these plants is thought to be an adaptation to a lack of nutrient availability, a common characteristic of bogs and waterlogged environments (Ellison & Gotelli, 2001). Nutrients derived from the captured and digested prey are assimilated into the plant. Captured prey consists mainly of Coleoptera,

Diptera, Hymenoptera (Green & Horner, 2007) and Lepidoptera (Cresswell, 1991; Heard, 1998; Newell & Nastase, 1998). While numerous previous studies have examined *Sarracenia* (Bennett & Ellison, 2009; Ellison, 2004; Schnell, 1978, 1983) in plants, few have studied and explained the role of color as an attractant. Red pigmentation in *Nepenthes ventricosa* Blanco, was found to have a significant effect in attracting more prey than plants with lesser pigmentation (Schaefer & Ruxton, 2007). Such was the



**Figure 3: Comparison of *Sarracenia* growth points between anthocyanin and anthocyanin free plants.**

findings of Newell & Nastase (1998) in *Sarracenia purpurea* L. which determined that red venation was responsible for attracting more insects. This red coloration was determined to be due to the presence of

anthocyanin, a flavonoid (Sheridan & Griesbach, 2001). However other studies have suggested that coloration was not responsible for prey attraction (Bennett & Ellison,

2009; Bennett, 2010) and that anthocyanin-free plants actually captured more prey mass than their red counterparts (Sheridan et. al., 2000).

Numerous color variations of *Sarracenia* have been found in the wild, including one entirely green form, an anthocyanin-free plant (Figure 2) (Schnell, 2002). This anthocyanin-free form occurs among the more common red pigmented plants (Schnell, 2002). Anthocyanin, a type of flavonoid, is responsible for the red pigmentation in the flowers and leaves of the genus *Sarracenia* (Sheridan & Griesbach, 2001). A



**Figure 4: *Sarracenia leucophylla* flowers depicting the anthocyanin free (left) and red (right) phenotypes. Taken from:**  
[http://www.plantarara.com/carnivoren\\_galerie/sarracenia/leucophylla/sarracenia%20leucophylla%20typ%20yellow%20flower%203.JPG](http://www.plantarara.com/carnivoren_galerie/sarracenia/leucophylla/sarracenia%20leucophylla%20typ%20yellow%20flower%203.JPG) and  
<http://www.sarracenia.com/photos/sarracenia/sarraleuco010.jpg>

dominant/recessive relationship is responsible for presence and absence in anthocyanin production respectively (Sheridan, 1997). The dominant allele results in the common expression of red pigmentation anywhere within the plant tissue, while the expression of the recessive allele results in a complete lack of anthocyanin expression (Figure 3) (Sheridan, 1997). The absence of anthocyanin becomes quite visible when comparing not just *Sarracenia* pitchers but also their flowers (Figure 4). The recessive allele does not prove lethal and results in a genetic variation within the population whether found in a heterozygous or homozygous allelic state (Sheridan & Mills, 1998). The presence or absence of anthocyanin pigment in *S. leucophylla* has yet to be conclusively linked to any effect in prey attraction or capture

and will be the focus of this study. Bennett & Ellison (2009) and Milne (2010) determined that prey capture in *Sarracenia purpurea* was not based on coloration of pitchers but rather on other means of attraction. If anthocyanin presence increases prey capture in comparison to anthocyanin absence, it could be hypothesized that wild-type red plants should have a selective advantage over green plants (Sheridan & Mills, 1998). However it is unlikely that red colored plants would have an increase in prey attraction based on Hymenoptera, Diptera, Coleoptera and Lepidoptera vision which cannot distinguish red pigments like the human eye (Schaefer & Ruxton, 2007; Briscoe & Chittka, 2001; Lall et. al., 1980; Snyder & Pask, 1973). Hymenoptera, Diptera and Coleoptera vision can detect the ultraviolet spectrum (Briscoe & Chittka, 2001) with a peak UV sensitivity of 340 nm (Peitsch et. al., 1992; Snyder & Pask, 1973). It is then likely that Hymenoptera can detect UV reflectance off of these pigments as the only UV absorption peaks of anthocyanin are 270nm-290nm (Woodall & Stewart, 1998). However anthocyanin has a secondary absorption peak at 530nm (Pirie, 1976) which Hymenoptera, Diptera, Coleoptera and Lepidoptera are able to detect. Based on this absorbance, and the ability of insects to detect this spectral range, it is then likely that this appears as a dark pattern to potential prey vision. However, Peter D'Amato noted that anthocyanin free plants consumed equal quantities of prey as red pigmented plants (D'Amato, Pers. Comm.). This was also the observation of Bennett (2010), who concluded that insect prey mass in *S. purpurea* was not affected by any ratio of visible red area.

*Sarracenia* pitchers have the unique trait of secreting extra floral nectar along their entire exterior surface from nectaries which become quite dense on the peristome, lids and pitcher throats (Figure 5) (Schnell, 2002). Insect visits are rewarded with this nectar, a substance high in carbohydrates, which tempts further exploration of the pitcher, especially along the pitcher throat (Juniper et al., 1989). The high absorption of UV light by this nectar suggests the use of nectar guides (Gloßner, 1992). Against the natural background of the pitcher, these dark patterns can be seen by Hymenoptera, Diptera,



**Figure 5: *Sarracenia* hybrid exhibiting a prime example of nectar aggregation along the throat.**

Coleoptera and Lepidoptera (Schaefer & Ruxton, 2007; Briscoe & Chittka, 2001; Lall et. al., 1980; Snyder & Pask, 1973) and likely serve as attractants which would make these nectar pools evident to potential prey (Joel, 1986; Joel et al., 1985). Additionally suggestions have been made that nectar, combined with various physical characteristics, such as taller and wider pitchers, results in higher prey attraction and capture rates (Bhattarai & Horner, 2009). However Milne (2010) has shown that plants lacking nectar secretion along the peristome are still

capable of insect capture. Physical traits of pitchers fluctuate readily within populations (Green & Horner, 2007). Thus it could be suggested that larger pitchers that are able to secrete larger quantities of nectar should have a selective advantage over smaller sized pitchers by attracting larger quantities of prey. Cresswell (1993) and Gibson (1991) found that larger pitchers were able to capture larger prey and consume greater quantities of

prey. This increase in prey capture was likely due to an increase in surface area which allowed for an increase in nectary allocation and not simply an increased size of the capture zone (Bhattarai & Horner, 2009). Newell & Nastate (1998) however, concluded that pitcher and plant size did not play any role in the number of visitors to pitchers. The current study will attempt to sort through these conflicting findings and more conclusively link the role of physical pitcher characteristics to the attraction of prey.

For the purpose of minimizing variability of nectary allocation, an F2 progeny of *S. leucophylla* resulting in red and green plants will be used. Using this population, nectary allocation variations will be potentially minimized as all plants share an identical gene pool. Additionally, it has not been observed that red plants secrete differing quantities of nectar than their green counterparts (Rice, Pers Comm, Sheridan, Pers Comm) and that extra floral nectary density in *Sarracenia* is 30-50 per mm<sup>2</sup> (Vogel, 1997; 1998a; 1998b). To ensure that nectary number is consistent, an assessment of nectary allocation will be performed on the two color morphs. By ruling out nectar as a varying factor, color will be isolated as the single differing trait and thoroughly assessed.

## Materials and Methods

Six separate groups of *Sarracenia leucophylla* containing a mixture of ten wild-type and ten anthocyanin-free specimens were grown side by side in separate outdoor plots for one growing season outdoors at Meadowview Biological Research Station (MBRS), Woodford, Virginia. Plots one through three (Young Group) were established spring 2011 from single, rooted, growth points while plots four through six (Old Group) were established at MBRS in 2009. The designation of a young and old group was chosen in order to double the sample size and cover a range of variation in regards to flowering. The young group, consisting only of single divisions, would be less likely to flower than the older group. Additionally, should the young group have flowering plants, the energy demand on the plant would be more costly than it would be to a larger plant. The energy used in flower production would be energy not used in the active growth of the plant, potentially leading to smaller pitchers in terms of height and mouth width.

A random number table was used to assign pot placement within the experimental design. Growth conditions were as follows:

1. Light regime consisted of a minimum of eight hours of direct natural sunlight.

The actual hours of sunlight per day changed according to the growing season.

2. In addition to natural rainfall, the water regime consisted of pumped water from the local pond into gravity fed tanks and water level maintained at one-third pot height.
3. Growth media consisted of premixed and pre-moistened 50:50 Canadian sphagnum peat moss and silica sand placed in gallon size circular pots
4. Prey consisted only of local fauna.

All pitchers were allowed to attract, capture and digest prey. All pitchers containing a distinguishable mouth, hood and peristome were harvested from each plant. Bags labeled with plot and pot number were filled with the individually labeled pitchers from appropriate pots. Pitcher height was measured to the nearest half centimeter, mouth width measured by a digital caliper to the nearest millimeter, and both measurements recorded.

Pitchers were cut then dried at Ball State University's herbarium drier to dehydrate pitcher and insect mass. Upon desiccation, pitchers were dissected and insect mass pooled for each individual pot and recorded with 0.001 g accuracy. Pitchers containing any holes chewed inwards out by captured prey, regardless of diameter, were recorded and their dry prey mass recorded. Pitchers containing pupae of *Isodontia mexicana*, grass-carrying wasp, were recorded as was the dry mass of the entire pitcher content as prey had been captured prior to pupae introduction. In addition, pitchers which may have fallen over for any reason prior to harvest were omitted as the quantity of

missing prey mass was unknown. Lastly, any pitchers missing a distinguishable lid or mouth were omitted.

Statistical analysis was performed using Minitab Statistical Software. Normality and sample variances were assessed for all tests performed. Based on these results, tests were performed as pooled. The following statistical tests were applied to the young and old groups with the exception of nectary count analysis which was carried out as a single test on a combination of both groups due to the labor and time required to assay each individual pitcher. While flowering, height and mouth width are factors dependent on the age of the plant, nectaries are present in all pitchers regardless of age. Two sample T-tests were used to determine whether temperature, nectary counts, prey mass, pitcher height and pitcher mouth width were different between red and green groups. Correlations were calculated between prey mass and pitcher height as well as prey mass and pitcher mouth width. Due to the large amount of statistical tests being performed and the testing for an overall null hypothesis, a Bonferroni adjustment was performed in order to adjust for the possibility of a false positive due to randomness. Alpha, 0.05, was divided by 9, the number of statistical tests testing red versus green in order to calculate the new alpha of 0.0055.

In order to conclusively rule out nectar as a varying factor, a nectary count was made on single pitchers for randomly selected pitchers amongst the six groups using a dissecting scope. Areas of one millimeter by one millimeter on pitcher throats were determined and nectary counts were recorded and a two-sample T-test performed.

Temperatures within pitcher traps were measured in October during mid-day in full sun using a thermocouple. Ten individual traps (five red, five green) from each plot were randomly selected and temperatures measured one inch deep within the pitcher. Due to the Q10 equation which states that chemical activity rate doubles with every 10° C increase, it is possible that red plants could potentially absorb and retain more sunlight than their green counterparts, thus increasing the internal temperature of the traps. This increase in internal temperature could give a higher decomposition rate in red plants leading to a decreased prey mass over green plants which lack red pigmentation.

The research questions and hypotheses are as follows:

Does anthocyanin have a significant effect on mass of insects captured by *Sarracenia* plants? It is hypothesized that anthocyanin presence in leaves of wild-type *Sarracenia* will be relevant in the attraction and predation of prey.

However, if anthocyanin pigment does not significantly affect capture mass, then the question becomes, does height and width of pitcher leaves play a role in mass of insect capture? In this case it is hypothesized that the increased height and width of pitchers will result in greater capture mass.

Does nectary allocation vary between anthocyanin free *S. leucophylla* and red *S. leucophylla*? It is hypothesized that nectary allocation will not vary between the two phenotypes due to using an F2 progeny from the same genetic cross.

Does temperature inside *S. leucophylla* pitchers vary between anthocyanin free and red phenotypes? It is hypothesized that temperatures will not vary between the two phenotypes.

## Results

Dried prey mass did not differ between red and green phenotypes for either group. Taller pitchers caught more prey mass, as did pitchers with wider mouths. There were very strong correlations between prey mass and pitcher height as well as between prey mass and pitcher mouth width. Temperature and nectary count were not different between red and green groups.

No significant differences were found between physical pitcher characteristics and dried prey mass amongst red and green plants in both the young and old groups (Table 1).

No significant differences were found between nectary count and temperature amongst red and green plants in both the young and old groups (Table 2).

All correlations for pitcher height and mouth width were found to be positively correlated with dried prey mass and significant (Table 3).

All correlation between pitcher height and pitcher mouth widths were found to be positively correlated and significant (Table 4).

	Height (cm)		Mouth Width (mm)		Prey Mass (g)	
Color	Red	Green	Red	Green	Red	Green
<b>Young</b>	36.49±0. 84	33.67±0.7 4	21.14±0.89	19.41±0.77	0.092±0.011	0.0669±0.0 085
<b>P-value</b>	p=0.013		p=0.144		p=0.076	
<b>Old</b>	40.01±0 .65	40.62±0.74	22.02±0.65	22.07±0.70	0.092±0.007	0.1009±0.0 094
<b>P-value</b>	p=0.541		p=0.955		p=0.478	

**Table 1:** Illustrated here are the means of the three primary physical factors measured for both red and green categories in the young and old groups. Listed p-values represent probability that the observed differences, between red and green plants in the category listed, were due only to random variation.

	Temperature (° C)				Nectary Count (#/mm <sup>2</sup> )	
Color	Red		Green		Red	Green
	Young	Old	Young	Old		
Mean	24.6	24.8	24.7	24.5	16.4	16.8
p-value	p=0.731		p=0.642		p=0.838	

**Table 2:** Illustrated here are the means for temperature and nectary count between red and green plants. P-value represents the probability that the observed differences were due only to random variation.

	Young		Old	
<b>Red Prey</b> <b>Mass (g)</b>	Red Height (cm)	Red Mouth Width (mm)	Red Height (cm)	Red Mouth Width (mm)
	r=0.674, p<0.001	r=0.882, p<0.001	r=0.473, p<0.001	r=0.555, p<0.001
<b>Green Prey</b> <b>Mass (g)</b>	Green Height (cm)	Green Mouth Width (mm)	Green Height (cm)	Green Mouth Width (mm)
	r=0.552, p<0.001	r=0.854, p<0.001	r=0.833, p<0.001	r=0.837, p<0.001

**Table 3:** The correlations between prey mass and physical factors of the same phenotype in both the young and old groups are shown here. P-value represents probability that the observed correlation between the two measured traits were due only to random variation.

Young		Old	
Red Height	Red Mouth Width	Red Height	Red Mouth Width
r=0.731, p<0.001		r=0.574, p<0.001	
Green Height	Green Mouth Width	Green Height	Green Mouth Width
r=0.653, p<0.001		r=0.608, p<0.001	

**Table 4:** The correlations between height and mouth width of the same phenotype within old and young groups are shown here. P-value represents probability that the observed correlation were due only to random variation.

## Discussion

There were no observed differences between red and green plants in either the young or the old group. All calculated correlations were positive and statistically significant.

*Statistical adjustments.*-The resulting p-value comparing height between red and green plants in the young group was 0.013 which would be statistically significant if the alpha threshold was 0.05. In theory, each and every test of significance performed has a 5% chance of producing a Type I error. Based on the multitude of statistical tests being performed to test a single overall null hypothesis, the use of a Bonferroni adjustment was a necessity to adjust for the increased likelihood that a false positive would arise due to random variation simply out of repetition. The Bonferroni procedure lowered the alpha to 0.0055 and enabled more conservative conclusions. Another factor taken into account was the use of large sample sizes (N=981). The larger a sample size, the more likely it becomes that small differences will be deemed statistically significant. Additionally, when examining the older group, plants had more time to grow and recover from transplant shock. This minimized the possibility that transplant shock would affect growth, possibly resulting in an incorrect conclusion.

*Physical traits.*- Pitcher height and mouth width did not differ between red and green phenotypes in either the young or old groups. This observation is likely best explained by the shared genetic pool of the plants. While the pitchers exhibited great variation in height and mouth width amongst each plant, both were essentially identical between red and green plants. This observation can also be applied to the nectary count and temperature which displayed no difference between green and red phenotypes. Based on the lack of difference in pitcher temperatures, the Q10 is likely to be unaffected by anthocyanin presence resulting in no difference in enzymatic activity. This is consistent with the findings of Green and Horner (2007) in *Sarracenia alata* Wood and Cresswell (1993) in *Sarracenia purpurea* L. though the morphologies of these three species differ greatly. Pitchers with larger mouth widths caught more prey mass than pitchers with smaller mouth widths. This relationship was explained by Green & Horner (2007) and Bhattarai & Horner (2009) as a factor of increased surface area for better display of attractants rather than an increase in the capture zone.

This study recorded a density of approximately 16 nectaries per mm<sup>2</sup> in *S. leucophylla* which differs from Vogel's (1998 a & b) findings of 30-50 nectaries per mm<sup>2</sup> in *S. purpurea*. While more research is needed to more conclusively explain this difference, we hypothesize that due to the low laying stature of *S. purpurea*, more nectaries are needed per mm<sup>2</sup> in order to appear more conspicuous and apparent against the ground to potential prey. This would not be the case with *Sarracenia leucophylla* which is able to stand high above the surrounding vegetation. Such a diminished amount of nectar production could be potentially beneficial by preserving energy.

*Correlates of prey capture.*— The correlations found between prey mass and pitcher height can be explained by the statement that a taller pitcher can not only absorb and hold more prey but can also advertise visual cues higher than shorter pitchers (Bhattacharai & Horner, 2010). Likewise, the correlation observed between prey mass and pitcher mouth width can be explained by the concept that pitchers with wider mouths are better able to advertise their nectar displays and make it more difficult for insects to gain a stable foothold across the entirety of the pitcher lip.

*Prey capture.* – No difference was noted between red and green phenotypes in either the young or old groups. There is no reason to suspect that prey mass should differ between phenotypes when taking into account prey vision and the lack of difference in pitcher height, mouth width, nectary count and temperature. This lack of difference may translate to a lack of fitness advantage in either phenotype, however future studies would need to validate this claim by examining reproductive capabilities in both phenotypes. While other studies have determined that nectary allocations were prominent on the ‘red veins’, we can conclude that prey vision did not display a preference for the presence of anthocyanin based on a lack of difference in capture rates.

Pitchers that were taller and had wider mouths caught more prey than shorter, smaller pitchers. This observation is best described by the findings of Green & Horner (2007) and Bhattacharai & Horner (2009) which describes the ability of taller and wider pitchers to better advertise the contrast of dark to light zones to potential prey. While in theory taller pitchers should catch more prey mass, pitchers were not allowed to collect

prey for the same duration of time through the growing season which resulted in a large variety of dried prey mass amongst pitchers of similar height. The same was true for pitcher mouths. Older pitchers which may have fully opened months prior to harvest would have had a longer window of opportunity to attract and capture prey than pitchers that may have opened a few weeks prior to harvest. However to combat this effect in both groups, a large sample size was used in order to minimize the effect of unequal predation times. Additionally the sole purpose of this study was to compare means between the phenotypes and not between different sized pitchers.

The lack of a difference in nectary count between red and green plants is possibly the most biologically important factor in this study. Based upon the results that red plants did not catch more prey than green ones and do not differ in height or mouth width, nectar is believed to be the main factor responsible for prey attraction (Joel, 1986). By ruling out anthocyanin as an attractant, this study confirms the conclusion of Bennett & Ellison (2009) which stated that prey was attracted to sugar and not color. Unlike nectar which rewards visiting prey and is easily visualized by signals of dark to light zones, the anthocyanin pigments do not reward visiting prey and can only be visualized by some species (Briscoe & Chittka, 2001). It is likely that the lack of UV reflectance in anthocyanin results in contrasting patterns which act as nectar guides, leading prey to nectar rich areas along the pitcher (Thompson, 1972). By examining insect vision and ruling out nectaries as a varying factor, this study was able to isolate anthocyanin and assess its potential role as an attractant. While Newell & Nastase's (1998) conclusion was correct, i.e. pitchers of *S. purpurea* with an increase in red venation had an increase in

prey attraction, future research should attempt to examine why the location of nectaries appears to be more prominent on these red venations of this species. In this study, pitchers on which nectary counts were done were all from the same gene pool. Thus it would be of interest for future studies to examine if nectary counts in *S. leucophylla* are different amongst different genetic pools.

## **Acknowledgments**

I would like to extend my deepest gratitude to my thesis committee, Dr. Donald Ruch, Dr. Phil Sheridan and Dr. Kemuel Badger for providing an invaluable source of knowledge and input on this paper. Without your revisions and insights, my journey to complete this project would certainly have met many more obstacles.

Thank you to Meadowview Biological Research Station for providing all materials, care, volunteers and housing during all of my trips out to Virginia.

Thank you to Ball State University for providing the herbarium, drying oven and necessary resources for proper analysis of samples.

To my wife to be, Amber, I thank you for your patience, understanding and help over these last two years. Your love and support kept me afloat through all my frustrations and challenges.

Lastly I would like to thank Joseph Meiring and all of the Meadowview Biological Research Station volunteers without whom the completion of this project would not have been possible. Your help was invaluable and your kindness will be forever cherished.

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