

Prey Capture in Anthocyanin-free *Sarracenia leucophylla* (Sarraceniaceae) Is Associated with Leaf Size, But Not Red Pigmentation

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Additional index words. anthocyanin, color, carnivorous plant, white-topped pitcher plant

Abstract. Anthocyanin pigmentation is a significant horticultural feature in plants and can be a crucial mediator of plant–insect interactions. In carnivorous plants, the modified leaves that capture prey can be visually striking and are traditionally considered prey attractants. Nevertheless, the question of whether bold color and venation patterns function as lures for insect prey remains ambiguous, and appears to vary across taxa. Furthermore, vegetative pigments can have alternate functions as protectants against thermal and oxidative damage. Our dual-year study compares the wild-type pitcher phenotype with a true-breeding anthocyanin-free mutant of the white-topped pitcher plant (*Sarracenia leucophylla* Raf.). We bred full-sibling crosses of *S. leucophylla* carrying either the wild-type anthocyanin gene or the anthocyanin-free variant. In both experimental years, growth points were established in outdoor plots and pitchers were allowed to capture prey before harvest at the end of each growing season. Dry weight of prey biomass was measured from pitchers of both pigment morphs, along with nectary counts, pitcher size, and internal temperature. The presence of anthocyanins in trapping leaves did not affect the biomass of insects captured. Nor did wild-type or anthocyanin-free pitcher morphs differ in size, temperature, or nectary counts. Instead, pitcher height, and, nominally, mouth diameter were better predictors of prey biomass. Despite striking visual differences in pitcher color, wild-type and anthocyanin-free plants did not catch significantly different quantities of prey. Our study provides empirical data that anthocyanin pigmentation in *S. leucophylla* does not affect the capture of prey biomass, and supports a growing body of literature showing that pigmentation traits serve in multiple contexts.

Striking color and visual contrasts are widespread across angiosperms, often functioning as attractants that mediate important plant–insect interactions such as pollination (Bradshaw and Schemske, 2003; Chittka and

Menzel, 1992; Lehrer, 1994; Papiorek et al., 2016). This diversity in color and pattern is often achieved through anthocyanins, a secondary metabolite of flavonoid biosynthesis that generates a range of reds, purples, and blues (Koes et al., 2005; Tanaka et al., 2008). Nevertheless, anthocyanins can also have alternate biological functions, including protection from ultraviolet damage, oxidative stress, or ectothermic warming (Sapir et al., 2006; Stiles et al., 2007; Winkel-Shirley, 2002). This latter feature, in which dark-colored flowers with anthocyanin pigments can be 2.5 °C warmer than ambient air, may be important for insect associates that prefer warmer flowers (Whitney and Chittka, 2007).

Carnivorous plants are of extensive horticultural interest (e.g., Anthony, 1992; Bartsch et al., 2014; Northcutt et al., 2012), and their modified leaves are used to capture insects for heterotrophic nutrients. The bold red contrasts and leaf venations are traditionally viewed much like floral visual signals to attract insects (e.g., Juniper et al., 1989) and there is some evidence supporting this hypothesis in both the North American (Sarraceniaceae) and Asian (Nepenthaceae) pitcher plants (e.g., Cresswell, 1993; Edwards, 1876; Jürgens et al., 2015; Newell and Nastase, 1998; Schaefer and Ruxton, 2008). In contrast, this relationship was not found in the adhesive trapping leaves of *Drosera* (Foot et al., 2014), nor in butterwort (*Pinguicula planifolia*), in which red leaves appeared to capture fewer prey than anthocyanin-free leaves (Annis et al., 2018).

In North American *Sarracenia* spp., pitcher leaves capture a wide variety of taxa, including hymenopterans, dipterans, and lepidopterans (Juniper et al., 1989). Spectral sensitivity of prey visual systems is highly variable, both across and within invertebrate orders (Briscoe and Chittka, 2001). Innate color preferences can also differ depending on ambient light, background illumination, and insect gender, making it difficult to predict the effect of pigmentation on insect capture (Kinoshita et al., 2017).

Nevertheless, pollination and attraction syndromes typically include an integrated suite of characters, and color traits may covary with other features such as morphology and nectar production (Fenster et al., 2004; Hermann et al., 2013; Stuurman et al., 2004), making it hard to ascertain the role of color and pattern in pitcher leaves. In *Sarracenia*, nectaries are located primarily along the peristome and around the opening of the pitcher mouth, and may increase the visitation time of insect prey (Juniper et al., 1989). Accordingly, the presence of nectar (although not necessarily the amount) (Bennett and Ellison, 2009) or pitcher size may be more salient than red coloration in capturing certain types of prey (Bhattacharai and Horner, 2009; Sheridan et al., 2000).

Sarracenia L. is an insectivorous genus distributed across wetlands in the United States and Canada (Mellichamp and Case, 2009). Wild-type plants typically have some degree of red coloration in netting and venation patterns across trapping leaves (“red”), which results from the production of a single anthocyaninidin: cyanidin (Sheridan and Griesbach, 2001; Sheridan and Mills, 1998b). Anthocyanin-free individuals persist in a number of wild populations, the result of a recessive, green phenotype from a late-stage mutation in the anthocyanin biosynthesis pathway (“green”) (Sheridan and Mills, 1998a).

A mutation blocking production of a single anthocyanin in the leaves of *Sarracenia leucophylla* offered a unique opportunity to test the role of anthocyanin in prey capture in *Sarracenia*. We used true breeding siblings of both red and green phenotypes in *S. leucophylla* (the white-topped pitcher plant) to determine how the presence of anthocyanin pigmentation 1) affected the biomass of prey

Received for publication 22 Mar. 2021. Accepted for publication 28 June 2021.

Published online 7 September 2021.

We gratefully acknowledge Duncan Connolly for experimental and technical support.

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capture, and whether this relationship was influenced by 2) nectary concentrations, and 3) thermoregulatory variables.

Materials and Methods

Breeding lines. Homozygous wild-type (red) and anthocyanin-free (green) parents (Fig. 1) were collected from the National Pitcher Plant Collection at Meadowview Biological Research Station. Because of the rarity of anthocyanin-free *S. leucophylla* both in the wild and in the National Collection, anthocyanin-free plants from the National Collection were crossed with wild-type individuals to create heterozygous F₁ progeny. At maturity, F₁ plants were back-crossed to the anthocyanin-free parent (a test cross), and both anthocyanin-free F₂ *S. leucophylla* and F₂ individuals of the wild-type phenotype were raised to maturity for our experiment. Pollination methods to achieve these crosses followed the work of Sheridan and Mills (1998a). All experimental plants were repotted and grown in a 50:50 peat and silica sand mixture in 1-gal pots.

Experimental design. Six outdoor beds with flow-through irrigation were each assigned 10 wild-type and 10 anthocyanin-free individuals, with each within-bed position assigned using a random number table. Plants were grown outdoors at Meadowview Biological Research Station in Woodford, VA (lat. 38.1°N, long. 77.4°W) and allowed to capture naturally occurring prey across the growing season. The experiment was replicated across 2 years: 2009 and 2011. All upright pitchers with a distinguishable mouth, hood, and peristome were harvested from each plant and dehydrated at the Ball State University herbarium. Pitchers and prey were dehydrated, and measurements of height, mouth width, and dry insect biomass were recorded.

Pitcher characteristics. Pitcher height was measured from the base of the leaf to the opening of the aperture. Pitcher mouth size was measured using calipers as the widest diameter at the pitcher rim. Nectaries were quantified using a dissecting scope and were



Fig. 1. Wild-type (red, left) and anthocyanin-free (green, right) phenotypes of *Sarracenia leucophylla*.

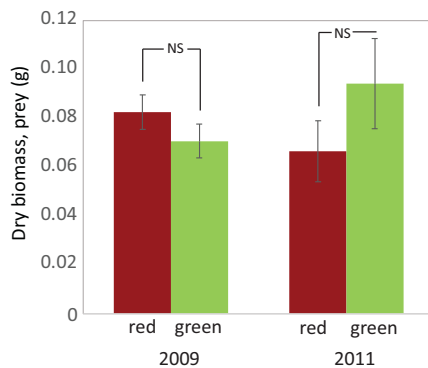


Fig. 2. Dry biomass of captured prey across wild-type (red) and anthocyanin-free (green) cultivars in 2009 and 2011. NS = not significant.

counted within a 1-mm² region from the throat region of randomly selected pitchers.

Temperature measurements. Temperatures were measured in full sunlight during midday in October. Thermocouples were placed 1 inch deep within the pitcher mouth, and temperatures recorded from five red and five green pitchers from separate individuals within each of the six plots.

Statistics. The effects of anthocyanin presence, pitcher height, and mouth width on prey mass were assessed separately for each year using general linear models. Size and mass were modeled as continuous variables for linear regressions. Color morph and year were analyzed as categorical factors in a two-factor analysis of variance using Statistica 7.0 (StatSoft, Inc., Tulsa, OK). Two-sample student *t* tests were used to compare pitcher traits, including temperature, across anthocyanin-free and wild-type pitcher morphs.

Results

Prey capture is unaffected by the absence of anthocyanins. There was no significant effect of anthocyanin presence on captured biomass in either year [$F_{2009(1,50)} = 0.26, P > 0.5$; $F_{2011(1,110)} = 1.7, P > 0.10$] (Fig. 2), nor did the effect of anthocyanins on prey capture differ across years [year-by-color interaction: $F_{(1,164)} = 3.48, P > 0.05$].

Strong effects of pitcher mouth size on prey capture. In both years, captured prey mass was best predicted by the width of the

mouth [$F_{2009(1,50)} = 26.7, P > 0.001$; $F_{2011(1,110)} = 47.2, P > 0.001$], explaining 64% of prey capture in 2009 and 72% of prey capture in 2011 (Fig. 3).

Nectary density did not differ across color morphs. When controlling for the size of pitcher throat areas, the density of nectaries did not differ across red (16.4/mm²) and green (16.8/mm²) color morphs ($P > 0.05$) (Table 1).

Pitcher traits did not differ significantly across wild-type and anthocyanin-free morphs. There were no differences in pitcher height, mouth width, and pitcher number between wild-type plants and anthocyanin-free cultivars (Table 1). Internal pitcher temperatures in both phenotypes averaged just under 25 °C (Table 1).

Discussion

In our study, we used controlled lines of true-breeding *S. leucophylla* to investigate phenotypic variability across wild-type and anthocyanin-free pitcher cultivars.

Does anthocyanin presence contribute to prey capture? Wild-type *S. leucophylla* pitchers, which had strong red venation patterns, captured similar amounts of prey when compared with anthocyanin-free green pitchers (Fig. 1). Historical work in *Darlingtonia californica* suggested that greater anthocyanin pigmentation was associated with increased prey capture (Edwards, 1876), whereas more recent experimental work showed that red venation in the attraction zone of decumbent *S. purpurea* pitchers correlates positively with the number of prey visits (Newell and Nastase, 1998) and prey captures (Cresswell, 1993). Furthermore, in *Nepenthes* spp., the hanging pitchers of *N. ventricosa* attracted more dipteran prey when colored red artificially, as compared with green-painted leaves (Schaefer and Ruxton, 2008). Nevertheless, our study results contrast with these findings, and instead support data from populations of *S. alata* Wood, which show no relationship between red hood contrasts and prey biomass (Bhattarai and Horner, 2009; Green and Horner, 2007), and data from *S. purpurea* (Bennett and Ellison, 2009; Milne, 2010), which reveal that color is less important than nectar in prey attraction. These contrasting

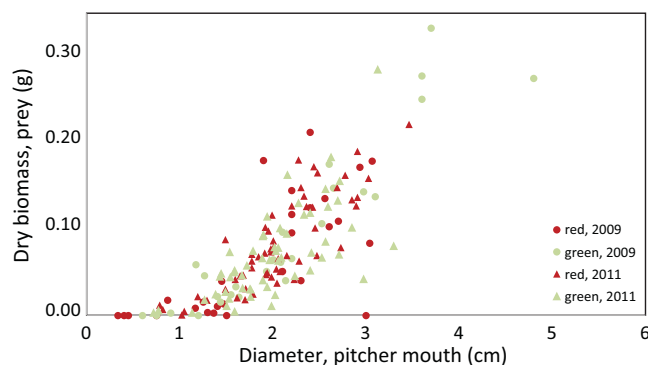


Fig. 3. Dry biomass of captured prey as a function of pitcher mouth diameter and cultivar in 2009 (circles) and 2011 (triangles).

Table 1. Phenotypic traits for wild-type (red) and anthocyanin-free (green) pitcher cultivars across two experimental seasons (mean \pm SE).

Yr	Pitcher no.		Ht (cm)		Mouth width (cm)		Temperature ($^{\circ}$ C)		Nectaries (no./mm ²)	
	Red	Green	Red	Green	Red	Green	Red	Green	Red	Green
2009	3.04 \pm 0.3	2.9 \pm 0.4	28.8 \pm 2.0	30.2 \pm 1.9	1.8 \pm 0.2	2.1 \pm 0.2	24.75 \pm 0.27	24.68 \pm 0.31	16.4 \pm 0.9	16.8 \pm 1.7
2011	8.0 \pm 0.9	8.2 \pm 0.8	36.9 \pm 2.0	36.2 \pm 2.0	2.0 \pm 0.07	2.0 \pm 0.07	NA	NA	NA	NA

For all traits, $t < 0.5$; $P > 0.05$.

NA = not applicable.

studies reveal a more complex interplay between pitcher plants and their insect associates, in which visual features may interact with gustatory and volatile cues (e.g., Jürgens et al., 2009) to capture prey animals. Indeed, geographic variation in prey composition and abundance, as well as climatic variables, may help explain the relative importance of each variable.

What is the role of anthocyanin pigmentation in Sarracenia? Despite a historical inclination to attribute anthocyanin coloration as a mechanism for insect capture in *Sarracenia*, our results suggest that anthocyanins do not perform that function. However, several alternative hypotheses exist for the continued presence of anthocyanins in *Sarracenia*. First, because floral color is determined in part by anthocyanin pigmentation, one possibility is that selection for the deep-red flowers of wild-type *S. leucophylla* leads to pleiotropic expression of anthocyanins in leaf patterns (Berardi et al., 2016). Second, measurements of dry insect biomass may not capture insect taxonomic composition accurately, which may have varied across red and green morphs, leading to differences in heterotrophic nutrient gain. We suggest further studies to understand these nonexclusive hypotheses.

We also found no differences in internal leaf temperatures in the study area between wild-type and anthocyanin-free pitchers. Warmer flowers (Herrera and Pozo, 2010), including darker flowers that trap solar radiation (Sapir et al., 2006), are thought to provide thermal rewards for visiting insects. In pitcher plants, increases in trap temperature would have important consequences for microbial decomposition and nutrient acquisition. In *Sarracenia*, for example, plants fed with supplemental prey showed altered nutrient ratios and increased photosystem efficiency. Nutrients from supplemental feeding also improved growth rates and resulted in proportionately more phyllodia when compared with unfed controls (Farnsworth and Ellison, 2007). Nevertheless, it is possible that by late fall, measurements of midday sun would have been less direct than earlier in the season, and that any thermal effects would be more salient in species with greater variation in lid morphology and color pattern. Temperatures in this area vary, on average, by 7 $^{\circ}$ C between July and October, and further studies of internal pitcher temperatures across the growing season would be especially informative.

Effects of pitcher size on prey capture. Pitcher size, which correlated highly with mouth width, explained much of the variation in prey mass. The effect of mouth width on prey capture is thought to result from several

possibilities: first, the width of the mouth correlates with greater probability of encounter, or second, the area of attraction is greater because there is a greater surface area for attractants, including extrafloral nectaries or scent volatiles. Because extrafloral nectaries can be confounded with venation (Bennett and Ellison, 2009; Cresswell, 1993; Newell and Nastase, 1998), and because a larger area of nectaries can attract insect clades selectively (e.g., ants) (Bennett and Ellison, 2009), we used sibling relationships from selectively bred F₂s to minimize variation in the genetic background between green and red individuals. This allowed our study to control for attractant area between the wild-type and anthocyanin-free groups. Indeed, we observed no difference in size, as measured by pitcher number, height, and mouth width (Table 1) across each cultivar, nor did nectary concentration differ across wild-type and anthocyanin-free phenotypes (Table 1).

Conclusion

Taken together, our study adds to an increasingly diverse number of species in the North American *Sarracenia* where prey capture depends strongly on pitcher size (Bhattarai and Horner, 2009; Cresswell 1993; Gibson, 1991; Green and Horner, 2007). Although we cannot yet rule out the role of volatile signals (e.g., Ho et al., 2017; Jürgens et al., 2009) on prey capture, and whether they will vary across wild-type and anthocyanin-free cultivars, other attractive features, including nectar, may serve different roles in attracting specific insect clades (e.g., ants) and may be more critical in the suspended pitcher plants of the Asian *Nepenthes* genera. The presence of fenestration and areolar patterns on pitcher leaves may also function as visual lures or as long-range attractants (e.g., McGregor et al., 2016; Schaefer and Ruxton, 2014). Finally, we consider that the presence of anthocyanins and flavonoid classes may be nonadaptive with respect to prey capture in this genus, and may subservise additional crucial roles in plant fertility and stress responses (Landi et al., 2015; Winkel-Shirley, 2002). For example, anthocyanins in cauline and leaf tissues can have photoprotective effects against high-intensity light stress (Gould et al., 2000, 2010), and can also play a role in alleviating water stress (Chalker-Scott, 1999), accumulating during periods of photo-oxidative and drought stress (e.g., González-Vilagra et al., 2019; Moustaka et al., 2020).

We emphasize that the ecosystems of the North American *Sarracenia* tend to be water-saturated, fire-maintained ecosystems.

Background contrasts are vastly important considerations for the perception of visual signals (Endler 1992), and may alter the way red and green contrasts are perceived. In addition, the particulate environment following small-scale vegetation fires and pollution may alter the scent background and insect composition substantially (e.g., Lusebrink et al., 2015). We encourage further studies to examine the complexity among plants, insect associates, and environmental variables in this diverse genus of plants.

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