EFFECTS OF POLLEN LIMITATION ON SEED PRODUCTION

IN THE PALE PITCHER PLANT (*SARRACENIA ALATA*)

By

KARIS KANG

Bachelor of Science, 2014
Andrews University
Berrien Springs, MI

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Introduction

Pollination is an essential process in maintaining ecosystems. Pollen is produced on the anthers (male organ) and transferred to the stigma (receptive female organ) via abiotic vectors such as wind or biotic vectors like insects, bats, and birds (Yang 2013). Once on the stigma, the pollen grains form pollen tubes which grow through the style to the ovary and through which the male gametes travel to fertilize ovules. This process of sexual reproduction contributes to the continuation and genetic diversity of populations from one generation to the next. Although animal reproduction is not typically limited by the availability of male gametes (Bateman 1948), studies have shown this does not always hold true for plants. If flowers receive an insufficient quantity of pollen (male gametes), fewer seeds or fruits may be produced (Bertness and Shumway 1992; Johnson 1991). This is known as pollen limitation (Ashman et al. 2004; Knight et al. 2005).

Though pollen limitation is typically recognized by a decreased quantity of offspring, it may also result in decreased quality of offspring (Baskin and Baskin 2018). Decreased pollen receipt may reduce competition among pollen grains to fertilize ovules, allowing pollen of lower quality (e.g., pollen with low genetic compatibility with the host plant) the opportunity to sire seeds where they might otherwise be outcompeted under conditions of higher pollen abundance. Decreases in offspring quality can be measured via embryo development (Sage and Sampson 2003), germination (Ranal and Santana 2006), and growth over multiple years (Sheridan and Karowe 2012). Thus, pollen limitation can affect not only population numbers, but also population resilience and individual fitness.

Pollen limitation and the causative factors vary by location, season, community, and species. Pollen availability can be affected by competition with other plants, population density, resource availability, habitat size and fragmentation, floral herbivores, and pollinators (Knight et al. 2005), as well as stochastic variation in the abiotic environment from season to season. Community-level interactions such as those between floral herbivores, pollinators, and seed predators can be especially challenging to

study, as each population is affected not only by other community members but also environmental factors specific to each population. As the importance of these community-level interactions becomes better understood and intersect with concerns about pollinator decline, shifts in population range, and phenology changes, the need for more empirical study in pollen limitation has become apparent (Cameron et al. 2011; Thomann et al. 2003; Thomas 2010; Zeng et al. 2011).

A large body of pollen limitation studies has accumulated on species of different life history traits and habitats (Larson and Barrett 2000). However, there have been few studies about the direct effect of pollen limitation on seed production in carnivorous plants. Only two studies have examined the effects of pollen abundance on reproduction of pitcher plants in North America - one on *Darlingtonia californica* found in California (Meindl and Mesler 2011) and the other on a population of *Sarracenia purpurea* in eastern Massachusetts (Ne'eman et al. 2006). No study has yet been done in any pitcher plant species from the southern United States or on the impact of floral herbivory on pitcher plant pollination. As potential habitat for pitcher plants diminishes with land-use changes (Folkerts et al. 1999), it is important to understand community-level interactions and changes in pollination as these may impact conservation efforts.

The focal species for this study, *Sarracenia alata*, the pale pitcher plant or yellow trumpet, is a host for the floral herbivore *Exyra semicrocea* and is found in seepage bogs in Texas, Louisiana, Mississippi, and Alabama. With one principal floral herbivore (Winer 2019) and one principal pollinator (*Bombus*) (Horner 2014), *S. alata* is well suited to serve as a model for the potential impact of floral damage and pollen limitation on pitcher plant seed production. Further understanding of pollination dynamics in this system would contribute towards management for stable *S. alata* populations, inform conservation for new or vulnerable populations that rely on seedling recruitment, and add to the larger field of pollen limitation research.

In this study, we addressed three questions: 1) Does floral herbivory decrease pollen abundance? 2) Does pollen limitation occur in this species? and 3) Does pollen limitation lead to decreased offspring fitness as measured by various measures of germination success?

Methods

Study Species*:*

Sarracenia alata is a carnivorous plant found in nutrient-poor bogs along the Gulf coast of the southern United States (Slack 2000). In the spring it produces a single pendulous flower with petals that interdigitate with a stylar umbrella, enclosing the anthers and the ovary, which consists of five locules. Pollen is released into the umbrella when the anthers dehisce (Figure 1). In order to enter and exit the flower, pollinators must crawl between the petals and stylar umbrella.
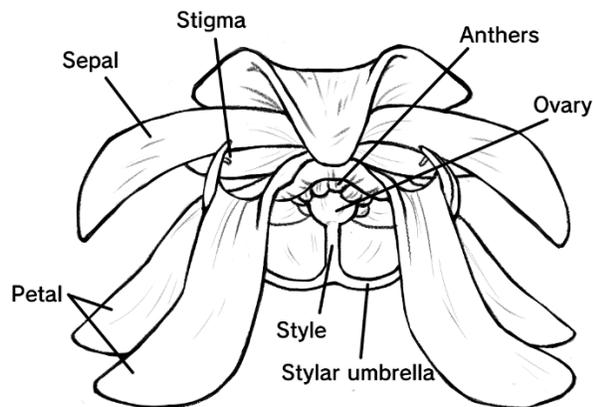
Figure 1. Cross-section of a Sarracenia alata flower. Anthers dehisce in the spring and drop pollen into the stylar umbrella. Pollen is then picked up by a pollinators (primarily Bombus*), which brush against the stigma of the next flower they visit. Illustration by Karis Kang.*

Exyra semicrocea is an herbivore that specializes on the genus *Sarracenia* (Jones 1907; Jones 1921; Stephens and Folkerts 2012). In the spring, the larvae feed on *S. alata* flowers before moving to the pitchers as they emerge and open (Winer 2019). When feeding on the flowers, the larvae typically consume the anthers before the other floral organs (Winer 2019).

Study Site:

We conducted experiments from April to September 2019 in a hillside seepage bog on private property in Leon County, Texas (31.54˚N, - 95.91˚W) (Carmickle and Horner 2019). The surrounding ecoregion is post oak savannah, populated by post oak (*Quercus stellata*) and loblolly pine (*Pinus taeda*) on sandy substrate (Carmickle and Horner 2019). Within the bog are willows (*Salix* spp.), maples (*Acer* spp.), various graminoids, and non-carnivorous forbs. Three carnivorous genera occur in the bog – sundews (*Drosera* spp.), bladderworts (*Utricularia* spp.), and our study species, *Sarracenia alata*.

Floral Herbivory:

We collected a total of 30 undamaged flowers and 26 herbivore-damaged flowers on April 14 (15 undamaged, 15 damaged) and April 19 (15 undamaged, 11 damaged) in 2019. Flowers were transported back to the lab, dissected, and the number of anthers was recorded for each flower within three days of collection. Anthers were then dried at 60 ℃ in a radiant heat oven for at least three days to ensure constant mass before anther dry mass was recorded for each flower. We compared anther count and anther dry mass per flower between damaged and undamaged flowers using a Kruskal-Wallis test. General linear models were used to determine whether collection date had any significant effect on anther count or dry mass.

The flowers within each of ten haphazardly placed 1-m^2 quadrats were counted and assessed for damage to the corolla, anthers, or ovary on April 19, 2019. A total of 139 flowers were surveyed.

Pollen Limitation:

On April 12 and 19, 2019, we haphazardly selected and assigned a total of 105 flowers to three treatment groups (35 flowers per group): pollen-limited flowers (low pollen), flowers receiving a naturally occurring pollen load (control pollen), and flowers supplied with pollen in addition to that naturally received from pollinators (high pollen). In order to ensure pollen limitation in the low-pollen group, pollinator exclusion bags were placed over young, partially unfurled flowers (visible stigmatic

umbrellas and petals that were not fully turgid), thus limiting the amount of time pollinators could access them. Flowers in the control group were unmanipulated and open to pollinators for the full flowering season. Flowers in the high-pollen group were open to pollinators and were also hand-pollinated using a pollen mixture collected from ten randomly selected donor flowers.

We collected ovaries from all flowers on September 29, 2019; 54% of low-pollen flowers (n = 19), 29% of control-pollen flowers (n = 10), and 17% of high-pollen flowers (n = 6) were recovered. Flowers were air dried in the lab at room temperature (ca. 21 °C) for at least three weeks before dissection. We recorded seed number, seed mass, and ovule number for each ovary. Proportion seed set (i.e., the proportion of ovules fertilized) was calculated as number of seeds / (numbers of seeds + ovules). Seeds and ovules from damaged ovaries were collected from intact locules. For ovaries with visible evidence of herbivore damage, values from intact locules were adjusted to five locules (the number in undamaged ovaries) to estimate the total ovary seed count, seed mass, and proportion seed set. Seed and ovule counts were gathered by scanning on an HP scanner at 600 ppi resolution and using ImageJ to count all particles that fell within pre-determined size and circularity ranges for seeds and ovules (seed size 0.6 - ∞ mm^2, circularity 0.4-0.9; ovule size 0.02-0.4 mm^2, circularity 0.5-0.98). Because sample sizes were so disparate among groups, we analyzed differences among treatments using Kruskal-Wallis tests.

Germination:

We conducted germination tests using ten seeds randomly selected from each ovary that produced at least 10 seeds. There were 8 ovaries in the low-pollen treatment, 8 ovaries in the control-pollen, and 6 ovaries in the high-pollen that produced at least 10 seeds. We rinsed ten seeds from each ovary in a 10% aqueous bleach solution for one minute in order to prevent mold growth. Seeds were then placed between sheets of filter paper dampened with DI water, stored in screw-cap vials, and cold stratified at 4 °C for two weeks (Ellison 2001). After stratification, we placed the seeds in a sterile petri dish on autoclaved agar. These plates were kept on a 12-hour light cycle at 21 °C in a growth chamber. Plates from all treatments were haphazardly dispersed throughout the chamber.

We recorded the number of germinated seeds (i.e., with the seed coat split) and the number of seeds with a protruding radicle in each of the 22 germination plates daily for 28 days. Plates with no germination were discarded if there were previous indications of ovary damage (e.g., mold) that may have interfered with germination. Altogether, 5 ovaries from low-pollen, 8 ovaries from control-pollen, and 5 ovaries from high-pollen produced usable results.

We compared differences for mean, median, and first day of germination and radicle appearance among treatments (Table 1). We also analyzed germination rate, proportion germination, and three measures of synchronicity (differences between first and last germination, first and last radicle appearance, and differences between germination and radicle appearance). All differences were analyzed using Kruskal-Wallis tests.

All statistics were performed in IBM SPSS Statistics 26 using an α-level of 0.05.

Table 1. Germination characteristics used to assess seed quality across three pollen treatments for Sarracenia alata (28 day trial).

Variable	Definition
Proportion of seeds germinated	Number of seeds germinated at the end of 28 days divided by the number of seeds plated (10)
First day of germination	Number of days after initiation of germination trial that the first seed germinated
Mean germination time	Sum of number of days to germination divided by the number of germinated seeds
Median germination day	Midpoint of the frequency distribution of days when seeds germinated

Synchronicity of germination	Difference in days between first and last germinated seed
Rate of germination	Number of seeds germinated divided by the number of days between the first and last day of germination
Proportion of seeds with radicle appearance	Number of seeds with radicles at the end of 28 days divided by number of seeds plated
First day of radicle appearance	Number of days after the initiation of germination trial that the first radicle appeared
Mean number of days for radicle appearance	Sum of number of days to radicle appearance divided by the number of seeds which put forth a radicle
Median number of days for radicle appearance	Midpoint of the frequency distribution of days when radicles appeared
Synchronicity of radicle appearance	Difference in number of days between first and last radicle appearance
Rate of radicle appearance	Number of seeds with radicles divided by the number of days between the first and last day of radicle appearance
Synchronicity of germination and radicle appearance	Difference in number of days between germination and radicle appearance

Results

Effects of Floral Herbivory on Pollen Availability

Collection date had no significant effect ($p > 0.05$) on anther number or anther dry mass per flower and data from both collection dates were combined for subsequent analysis. Herbivore-damaged flowers had significantly fewer anthers than in undamaged flowers (Figure 2A). Herbivore-damaged flowers also had significantly lower anther dry mass compared to undamaged flowers (Figure 2B). However, it should be noted that less than 2% of 139 flowers surveyed showed signs of florivory.
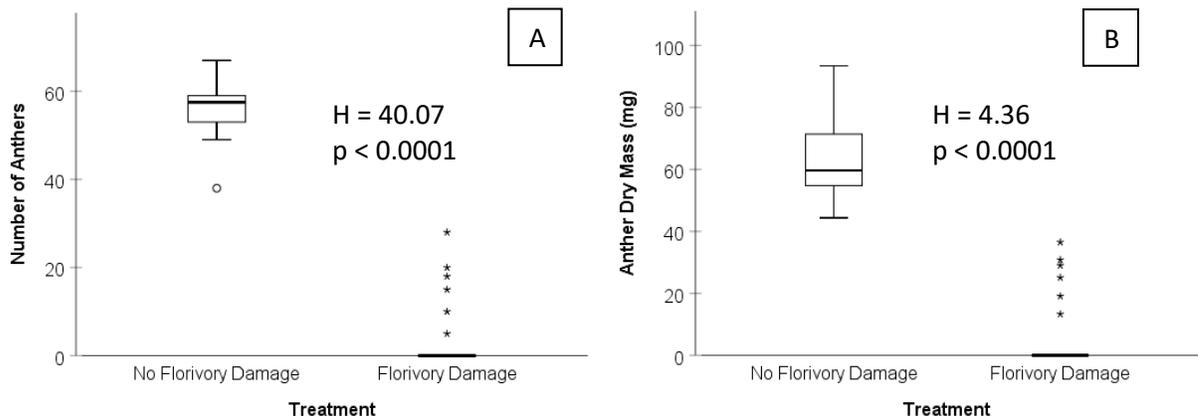
Figure 2. Anther count (A) and dry mass of all anthers (B) per flower for herbivore-damaged flowers (n=26) and undamaged flowers (n=30) of Sarracenia alata*; horizontal lines represent medians, boxes represent 1st and 4th quartiles, bars represent minimum and maximum values excluding outliers, points represent outliers.*

Effects of Pollen Availability on Seed Quantity

The high-pollen group had a significantly higher proportion seed set when compared with the low-pollen and control-pollen groups (Figure 3). The control-pollen group did not have a significantly different proportion seed set compared to the low-pollen group.
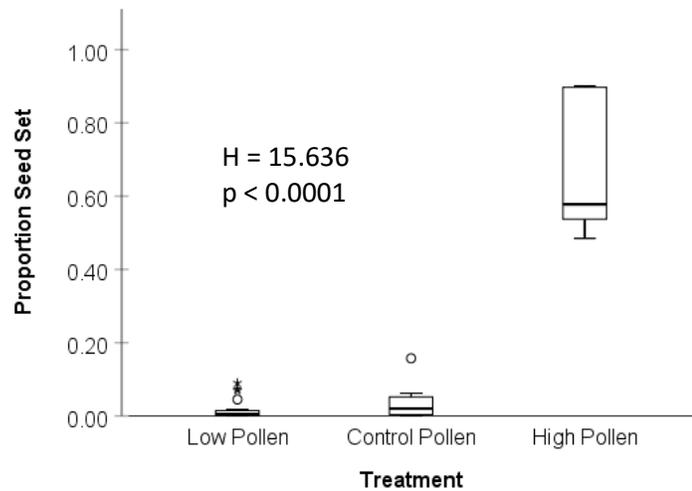
*Figure 3. Figure 3. Proportion seed set per Sarracenia alata flower for high pollen (n=6), low pollen (n= 19), and control pollen (n=10) treatments; lines represent medians, boxes represent 1st and 4th quartiles, bars represent minimum and maximum values excluding outliers, points represent outliers.*

The high-pollen group had significantly higher seed number and total seed mass per ovary when compared with the low-pollen and control-pollen group (Figure 4A, B). The control-pollen group was not significantly different from the low-pollen group for either variable. There were no differences among treatments for mass/seed (Figure 5).
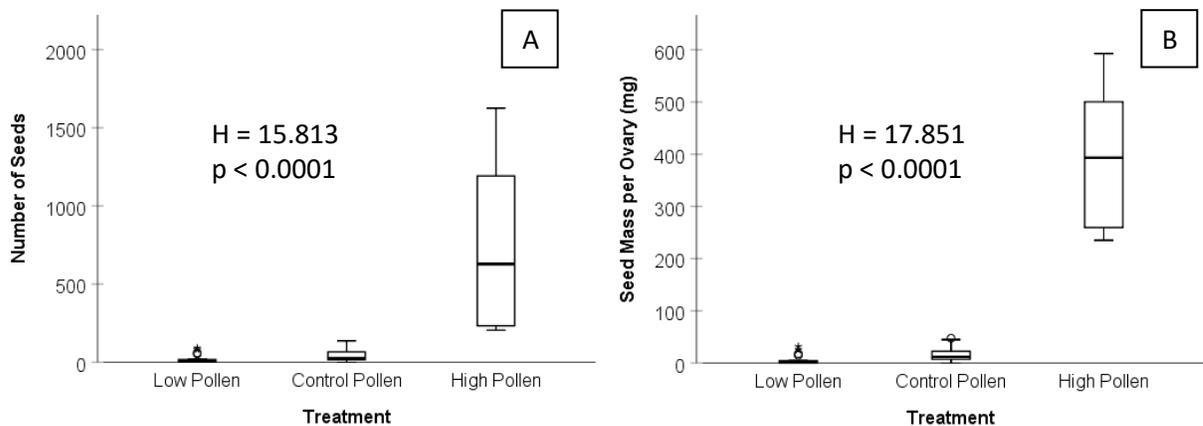

Figure 4. Number of seeds (A) and seed mass (B) per ovary for high pollen (n=6), low pollen (n=19), and control pollen (n=10) treatments in Sarracenia alata. *Horizontal lines represent medians, boxes represent 1st and 4th quartiles, bars represent minimum and maximum values excluding outliers, points represent outliers.*
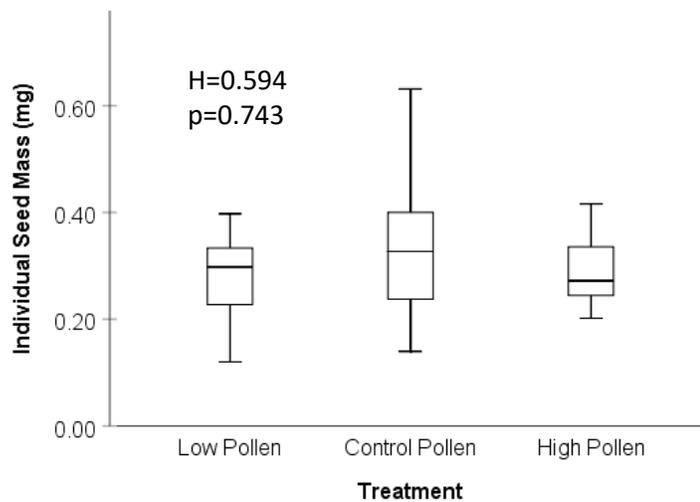
Figure 5. Individual seed mass for high pollen (n=6), low pollen (n= 13), and control pollen (n=9) groups in Sarracenia alata*; lines represent medians, boxes represent 1st and 4th quartiles, bars represent minimum and maximum values excluding outliers, points represent outliers.*

Effects of Pollen Availability on Germination Characteristics

There were no significant differences among treatments for proportion of seeds germinated, proportion of seeds with radicle appearance, first days for germination and radicle appearance, or mean and median germination and radicle appearance days (Table 2). There were also no significant differences detected among treatments for germination rate, synchronicity in germination, synchronicity in radicle appearance, or synchronicity between germination and radicle appearance dates (Table 2).

Table 2. Measures of Sarracenia alata seed quality and their associated test statistics and significance values. Variable definitions are given in Table 1

Variable Measured	H-Statistic	p
Proportion of seeds germinated	3.850	0.146
First day of germination	2.56	0.278
Mean germination day	2.37	0.306
Median germination day	1.387	0.5

Synchronicity of germination	3.509	0.173
Rate of germination	0.551	0.759
Proportion of seeds with radicle appearance	4.253	0.119
First day of radicle appearance	3.605	0.165
Mean number of days for radicle appearance	1.555	0.46
Median number of days for radicle appearance	1.265	0.531
Synchronicity of radicle appearance	3.823	0.148
Rate of radicle appearance	5.744	0.057
Synchronicity of germination and radicle appearance	2.81	0.245

Discussion

One potential cause of pollen limitation is floral herbivory, which impacts fitness directly via gamete consumption (Winer 2019) and indirectly by reducing pollinator visitation (Cunningham 1995; Krupnick et al 1999; Lohman et al 1996). Although low pollinator numbers in 2019 disallowed for examination of these indirect effects, we found that floral herbivory by *Exyra semicrocea* significantly decreased the number of anthers and, therefore, the quantity of pollen (male gametes) in a flower before pollen could be distributed, with damaged flowers losing on average 91% of anther dry mass compared to undamaged flowers. This loss is greater than the losses reported by Winer (2019); 50-80% of anther mass was lost during the 2017 and 2018 flowering seasons at the same field site.

These differences in anther consumption are part of a larger pattern of variation that includes proportion of total flowers attacked and types of floral damage. Quadrat sampling from previous years estimated that 53% of flowers were attacked in 2017 and 33% of flowers attacked in 2018 (Winer and Horner, unpublished manuscript), compared to < 2% of flowers attacked in 2019, the year of our study. Damage to floral parts also differed among the years, with primarily anthers showing significant damage in 2017 and all floral parts (ovary, anthers, and corolla) showing significant damage in 2018. In comparison, the few flowers that were damaged in 2019 showed mostly anther consumption. This variation among years may be due to differences in pitcher emergence times, as *Exyra* moves from the flowers to pitchers, their preferred food source, as soon as the pitchers open. Although pitchers usually emerge a few weeks after the flowers (Horner 2014), in 2019 pitchers and flowers could be seen emerging synchronously, which may have caused the larvae to move away from the flowers before causing much damage. Associations between pitcher phenology, herbivore populations, and floral damage bear further study.

Although there was less floral damage in 2019 compared to previous years, the number of seeds produced by naturally pollinated control flowers was significantly lower compared to flowers given supplemental pollen. This difference in seed output between control and high-pollen treatments indicate that pollen limitation occurred this year. However, it is important to note that although pollen supplementation has been a standard approach in determining pollen limitation, supplementation in one year alone cannot clearly differentiate among limitation in pollen quantity and pollen quality (Aizen and Harder 2007). However, proportion seed set in 2019 was also significantly lower than in previous years at the same site. Proportion seed set was 0.74 in 2015 and 0.69 in 2016 (Brilleslyper 2019). In comparison, average proportion seed set for unmanipulated flowers was 0.11 in 2019. This suggests that the observed difference between control and high-pollen treatments was not just an artificially inflated effect caused by experimental manipulation, but a clear indicator that pollen limitation occurred during the 2019 flowering season.

The low seed production after a spring of low floral herbivory also suggests that floral herbivores, which impact pollen quantity before dispersal, were not the primary factor influencing pollen limitation this year. During our field season, pollinator sightings were unexpectedly low compared to previous years (Horner, personal observation). In other plant species, fewer pollinators have been associated with greater pollen limitation and lower rates of outcrossing, with potential for long-term population decline (Anderson et al 2011; Moeller et al 2012; Pauw and Bond 2011). Although global pollinator decline has become a high profile conservation concern within the past decade (Thomann et al 2013) and broad-scale patterns of bumblebee decline have been identified in both Europe and North America (Grixti et al 2009; Cameron et al 2011), there is still a lack of regional data in many parts of the United States, including Texas (Warriner 2012). More empirical evidence is needed to identify whether pollinator decline is occurring locally, what multi-trophic relationships exist between fluctuations in pollinators, floral herbivores, and seed production, and the effects of pollen limitation on recruitment and offspring quality.

We began to address the effects of pollen limitation on offspring quality by using germination as an assessment of seed quality. Other studies have indicated that lower pollen quality, such as that resulting from self-pollination, can lead to less robust offspring (Aizen and Harder 2007; Sheridan and Karowe 2012). We hypothesized that pollen limitation could lower competition among pollen grains, providing opportunity for lower quality pollen to fertilize ovules where they might not under conditions of abundant pollen (Christopher et al 2020).

Our results did not reveal any significant difference in germination among treatments during the first four weeks of germination using the benchmarks (e.g., day of germination, rate, proportion of germination success, synchronicity) we analyzed. While this timeframe captures the first few weeks of germination, it overlooks longer-term effects that might be apparent during establishment or the course of a lifetime. Experiments with *Sarracenia flava* have shown differences in offspring quality between outcrossed and self-fertilized individuals when assessed over multiple years (Sheridan and Karowe 2012).

However, there have been no similar experiments on the effects of different levels of pollen receipt on offspring quality at different life stages in N. American pitcher plants.

Pollen limitation has been a growing field of study for the past few decades. Experiments have been conducted on a wide variety of species, with each study examining the causes and circumstances of pollen limitation unique to each habitat (Christopher et al 2020; Knight et al 2005). With one principal floral herbivore, *Exyra semicrocea*, and one known pollinator, *Bombus*, *Sarracenia alata* provides an opportunity to examine the effects of multi-trophic interactions on pollen limitation in a carnivorous plant, a group of plants where pollen dynamics are still not fully understood. In light of the decline in pollinator populations together with diminishing habitat, future experiments should further quantify what community-level dynamics may contribute to pollen limitation in this species, as well as what its long-term effects on population fitness may be. Understanding the forces that contribute to pollen limitation in this species and the potential effects on selection and population fitness would both fill a gap in the field of pollination studies and contribute towards conservation efforts for this unique and charismatic species.

Conclusion

Pollen receipt on stigmatic surfaces can be reduced by floral herbivores before dispersal and by low pollinator numbers during dispersal. In the study population of *Sarracenia alata*, floral herbivory significantly reduced pollen abundance in damaged flowers compared to undamaged flowers, although the proportion of damaged flowers in the population was lower than in previous years. Pollen supplementation increased the number of seeds produced and limiting pollen receipt decreased the number of seeds produced. However, pollen limitation occurred in naturally pollinated flowers even when floral damage for the year had been low, suggesting that pollen limitation was caused not by floral damage but by low pollinator visitation. Pollen limitation did not have a detectable effect on offspring fitness as measured during the first 28 days of germination.

Future work should explore pollinator decline as a potential cause of pollen limitation in *S. alata*, as well as the effects of pollen limitation on offspring quality during establishment and later life stages. Comparing the fitness of outcrossed versus self-pollinated offspring would give a clearer picture of the selective pressures at work between offspring quantity versus offspring quality. Further monitoring should also be done in order to determine whether pollen limitation in this population fluctuates naturally from year to year or whether a sustained decline in pollination is occurring.

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Vita

Personal
Background

Karis Kang

Saint Joseph, Michigan

Child of Sophia and Hyung-Chil Kang

Education

Diploma, Saint Joseph High School, Saint Joseph,
Michigan, 2011

Bachelor of Science, Biology, Andrews University,
Berrien Springs, 2014

Master of Science, Biology, Texas Christian University,
Fort Worth, 2020

Experience

English Language Teacher, South Korea, 2015-2016

Conservation Worker, Americorp,
Flagstaff, 2016

Conservation and Land Management Intern, Chicago Botanic Garden
Framingham, 2017

Teaching Assistantship, Texas Christian University
Fort Worth, 2018-2020

Abstract

EFFECTS OF POLLEN LIMITATION ON SEED PRODUCTION
IN THE PALE PITCHER PLANT (*SARRACENIA ALATA*)

By Karis Kang, M.S., 2020
Department of Biology
Texas Christian University

Thesis Advisor: Dr. John Horner, Professor of Biology

Pollen transfer among flowers contributes to genetic diversity and the maintenance of plant populations through the production of seeds. Decreased pollen receipt can result in fewer offspring. This is known as pollen limitation. We conducted field and laboratory experiments in a population of *Sarracenia alata* in Leon County, Texas in 2019 to examine 1) the effect of floral herbivory by the pitcher plant moth, *Exyra semicrocea,* on pollen availability and 2) the impact of pollen receipt on seed quantity and 3) seed quality. We found that floral herbivory significantly decreased the number and mass of anthers in flowers, and that a high pollen load significantly increased the number of seeds produced compared to low-pollen and control flowers. We found no differences in offspring quality among different pollen treatments based on germination traits. Pollen limitation occurs in *S. alata* and may pose a conservation risk when paired with other ecological disturbances.