Overcompensation by Pitcher's thistle (*Cirsium pitcheri*) in response to damage

Christopher Dao

6314 Boulder Drive

Flushing, MI 48433

cdao@umich.edu

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ABSTRACT

There has been evidence that plants exhibit overcompensation after damage through trampling or herbivory. *Cirsium pitcheri* is an endangered thistle found in the sandy dunes of northern Michigan. The purpose of our experiment was to determine if this monocarpic plant exhibits overcompensation by observing pollination and fitness measures. We recorded pollinator activity, head count, and seed output for both multi-stemmed plants, which are a result of damage, and single-stemmed plants at Sturgeon Bay in Emmet County, Michigan. We found that multi-stemmed plants have a higher number of pollinators as well as longer pollination time than single-stemmed plants. We also found that multi-stemmed plants produced about twice as many heads than single-stemmed. Lastly, we determined that although both groups of *C. pitcheri* contain about the same number of filled seeds per head, multi-stemmed plants produce much more seeds per plant, which is evidence for overcompensation. We believe that *C. pitcheri* responds positively to damage by exhibiting higher pollination activity and a greater seed output.

INTRODUCTION

Herbivores can be a threat to the growth, survival, and reproduction of plants. However, plants have developed defenses such as thorns or chemical poisons in order to deter herbivory or to recover from it. Tolerance or compensation, the ability to maintain fitness after sustaining damage, is a defense mechanism seen in some plants to cope with the damage caused by herbivores (Bergelson and Juenger, 1997). Although numerous studies have shown that there is no benefit of grazed plants to herbivory (Belsky, 1986; Bergelson and Crawley, 1992a, 1992b), plants may receive benefits from the organisms that eat them by positively impacting the growth of the plant in the long term which is considered overcompensation (Owen, 1980). An example of a plant that exhibits overcompensation in response to herbivory is scarlet gilia (*Ipomopsis aggregata*), which can regrow and produce additional flowering stalks and a higher amount of biomass (Becklin and Kirkpatrick, 2006). Individuals of *I. aggregata* that have been browsed by herbivores were shown to produce up to three times as many flowers, seeds, and fruits compared to the uneaten control plants (Paige and Whitham, 1987).

Besides producing additional stems, another important factor in the reproductive success of a plant is pollination. For many plants, pollination by animals is needed and can increase a plant's viable seed set (Steffen-Dewenter and Tscharntke, 1999). In order for overcompensation to occur, plants must produce a greater output of seeds after being damaged compared to before the impact. A plant's overall reproductive success can be increased with a higher quality of pollination and thus a higher amount of flower visits (Dauber et al., 2009). Bumblebees (*Bombus hypocrita sapporensis*) spent more time on large flowers than they did on small floral displays (Ishii, 1996). This showed that an increase in floral display can attract more insects visiting the plant and can help pollinate, thus producing a greater number of seeds.

Pitcher's thistle (*Cirsium pitcheri*) is a rare species that is only found in sandy dunes of the Great Lakes region of the United States and Ontario, Canada (Bell et al., 2002). It takes four to eight years to mature, and it is a monocarpic species, meaning that it dies after flowering (Hamze and Jolls, 2000). *C. pitcheri* is pollinated mostly by bees and other insects (Keddy and Keddy, 1988). This plant is federally threatened because of its high potential to become extinct and endangerment to its habitat (Pavlovic et al., 2000). Another potential threat to *C. pitcheri* is a non-native weevil, *Larinus planus*, which feeds on many native thistles (Louda et al., 2005). However, *L. planus* was detected to have a severe impact on *C. pitcheri* even though it was introduced as a biocontrol of other harmful and unpleasant thistles (Havens et al., 2012).

Our study focused on the fitness differences between multi-stemmed *C. pitcheri*, which is the result of damage including herbivory, and single-stemmed *C. pitcheri*. We asked (i) if there was a difference in the number of insect visitors and pollination time between multi-stemmed and single-stemmed plants, and (ii) if there was a significant difference in the reproductive output between the two groups of plants. We predicted that damage to *C. pitcheri* would result in overcompensation by producing more flowers, exhibit more pollination, and produce a greater amount of seeds. To determine this, we observed the differences in pollinator activity and fitness measures between damaged and undamaged plants. More specifically, we compared the total number of pollinators and the total visitation time on each plant. We also compared the number of heads per plant, size of heads, number of flowers per plant, as well as number of seeds per head and per plant. Ultimately, our goal was to determine if *C. pitcheri* displays either compensation or overcompensation in response to damage, including herbivory.

MATERIALS AND METHODS

The members of our group consisted of ecology students at the University of Michigan's Biological Station and included Julia Kehoe, Jordan McMahon, Araceli Morales-Santos, and me. Our study was performed near the shore of Sturgeon Bay, Lake Michigan in Wilderness State Park in Emmett County between July 16th and July 25th, 2013. We sampled a 50m x 50m plot that included the primary foredune and backdune and contained an adequate number of single-stemmed and multi-stemmed *C. pitcheri*. The terrain was sandy and inhabited by shorter vegetation including Marram grass (*Ammophila arenaria*), goldenrod (*Solidago houghtonii*), and sand cherry (*Prunus pumila*). In the plot, we marked each individual of *C. pitcheri* that was old enough to flower and sampled both multi-stemmed and single-stemmed plants.

We took down observations of pollinators on *C. pitcheri* by watching each plant for 10 minutes. It was important to remain a reasonable distance (~4ft.) away from the plant as to not disturb or deter any potential pollinators. We identified the types of insects that visited the plants, the number of pollinators that came, and recorded how much time each pollinator spent on the flowers of an individual plant. If the pollinator moved from one flower to another on the same plant, the time recorded was not stopped and continued. The pollination time of each insect visitor was added for a total visitation time spent on each plant.

For each individual *C. pitcheri*, we counted the number of total heads, heads >12mm, and heads <12mm, and measured the diameter of each head >12mm. If the head was <12mm, it was not considered to ever have the potential to flower in its future. We also determined the maturity stage of each head (stages 0-6) with stage 0 not yet bloomed and still closed, stage 1 just beginning to open, stages 2-5 in the process of blooming, and stage 6 past flowering. We removed heads (eight from multi-stemmed and eight from single-stemmed) in stage 6 that had not yet dispersed its seeds in order to count the number of filled and unfilled seeds in each head and found the average for multi-stemmed and single-stemmed. Using this data, we calculated the number of filled seeds per head >12mm as well as the number of filled seeds per plant, which we considered to be the reproductive output of the plant.

The mean number of potential pollinators, total pollination time spent on each plant, and number of pollinators per flowering head were compared between multi- and single-stemmed plants. Tests were performed to compare the following: total number of heads, number of heads >12mm, diameter of heads >12mm, number of flowering heads (stages 2-5), number of heads <12mm, and percentage of heads <12mm between multi-stemmed and single-stemmed plants. We used tests to compare the average number of filled seeds per head and finally the number of filled seeds per plant between multi-stemmed and single-stemmed *C. pitcheri*. A Chi square analysis was done using the frequency of heads in each stage of maturity to observe any differences in the timing of flowering between multi-stemmed and single stemmed plants.

RESULTS

Our plot contained a total of 34 *C. pitcheri* plants, 23 multi-stemmed and 11 single-stemmed. We noticed that multi-stemmed plants were closer in proximity with one another whereas single-stemmed plants were found by themselves more often. Also, the amount of sunlight, temperature, and wind speed could have had an effect on the pollinators since we performed our fieldwork on the site across multiple days.

We found significant differences in potential pollinators between multi-stemmed and single-stemmed *C. pitcheri* including total number of insect visitors (t = 2.888, df = 31.535, p-value = 0.0035; Fig.1) and total visitation time (t = 2.896, df = 26.133, p-value = 0.004; Fig.2).

There was a large variation in the total visitation time within each plant group with a range of 891s in multi-stemmed and 179s in single-stemmed plants, but there were two outliers where a couple of insects stayed on the flowers of multi-stemmed plants for over 10 minutes. The number of potential pollinators per flowering head was not significantly different between both groups (t = 1.086, df = 21, p-value = 0.145; Fig.1). The mean total number of potential pollinators in single-stemmed plants was 0.7±0.36 and in multi-stemmed it was 2.4±0.47, which was more than triple. Single stemmed plants had an average total visitation time of 27.5±16.43 seconds while multi-stemmed were much higher at 183.7±51.34 seconds per plant.

The number of heads <12mm (t = 1.964, df = 31.584, p-value = 0.029; Fig.3), number of heads >12mm (t = 2.973, df = 32, p-value = 0.003; Fig.3), and total number of heads (t = 2.891, df = 32, p-value = 0.0035; Fig.3) were also significantly different. Single-stemmed plants had an average of 1.8±0.67 heads <12mm, 6±1.08 heads >12mm, and 7.8±1.4 total heads. On the other hand, multi-stemmed *C. pitcheri* had a mean 4±0.88 heads <12mm, 10.8±0.99 heads >12mm, and 14.8±1.53 total number of heads. Multi-stemmed plants had almost double the number of heads across all categories compared to single-stemmed plants. There was a wide range in the total number of heads, which was 3-30 in multi-stemmed plants and 3-11 in single-stemmed plants. However, the number of flowering heads did not differ significantly (t=1.494, df=21, p-value=0.075; Fig.3). Only 17 of the 23 multi-stemmed *C. pitcheri* had heads that were flowering while 6 out of 11 single-stemmed plants were flowering. There was not a significant difference in the percentage of heads <12mm (t = 0.664, df = 32, p-value = 0.256) with multi-stemmed being 23% and single-stemmed 18.3% comprised of small heads. The size of heads among each group of plant did not differ significantly (t = 0.773, df = 123.714, p-value = 0.221) with multi-stemmed plants having a mean diameter of 17.49±0.2mm and 17.21±0.31mm for single-stemmed *C. pitcheri*. The result of the Chi square analysis of the stages of heads between multi-stemmed and single-stemmed was not significant (χ^2 = 3.276, df = 7, p-value = 0.8; Fig.4).

The average total number of seeds per head was 91.1 for single-stemmed and 91.3 for multi-stemmed. Single-stemmed plants had less filled seeds per head >12mm on average with 50.9±7.88 while multi-stemmed contained 62.2±11.18 seeds, but this did not show a significant difference (t = 0.846, df = 11, p-value = 0.416; Fig.5). However, there was a significant difference in reproductive output between single-stemmed and multi-stemmed *C. pitcheri*, which was measured in number of filled seeds per plant (t = 4.454, df = 29.713, p-value < 0.001; Fig.6). The mean number of filled seeds per single-stemmed plant was 305.2±54.86 seeds, and the mean number of filled seeds per multi-stemmed plant was 673.1±61.76 seeds. The range in the number of seeds was 932.6 per multi-stemmed plant and 559.5 per single-stemmed plant on average.

DISCUSSION

Pollinators are very important to *C. pitcheri* because this is the only way they can reproduce since they cannot undergo vegetative reproduction (Hamze and Jolls, 2000). Since multi-stemmed plants had a significantly higher number of potential pollinators and total visitation time by insects, this could contribute to the higher reproductive success of multi-stemmed *C. pitcheri* over single-stemmed. The significant difference in visitation time per flowering head also shows that potential pollinators are spending more time on the individual flowers on multi-stemmed plants than they are on single-stemmed. For small populations, similar to *C. pitcheri* at Sturgeon Bay, there was an effect of patch area and density of flowers on insect visitation (Dauber et al., 2010). Although the difference in number of flowers per plant was insignificant, there was an increasing trend in number of flowers from single-stemmed to multi-stemmed. Also, we noticed that multi-stemmed plants were closer together in proximity than single-stemmed plants. A greater patch area and higher density of flowers among multiple plants could be why multi-stemmed *C. pitcheri* were found to have more potential pollinators and greater pollination time.

Multi-stemmed plants have just about double the number of heads <12mm, heads >12mm, and total heads in comparison with single-stemmed plants, which could have both its advantages and disadvantages. Since multi-stemmed plants have a greater total number of heads and heads >12mm, this gives the plant more opportunities for flowering. However, since multi-stemmed plants also have double the number of heads <12mm, which will most likely never bloom, this means that the plant is expending a lot of extra energy into producing heads that are not used. An increased expenditure of resources for pollinator attraction, like the production of large heads, should reduce allocation to other activities, like the production of small heads (Andersson, 2006). But by comparing the percentage of small heads between single-stemmed and multi-stemmed, the insignificant difference tells us that both groups of plants are spending about the same amount of energy in proportion to the number of total heads the plant possesses. The size of heads between multi-stemmed and single-stemmed did not differ significantly, which tells us that although there are more heads on multi-stemmed plants, single-stemmed plants are not utilizing the extra energy into producing greater heads to create larger flowers for more insect visitors and an increased visitation time by pollinators (Ishii, 2006). By comparing the stages of heads between multi-stemmed and single-stemmed plants using the Chi-square analysis, we found that both groups of plants are maturing at the same rate. Having a similar phenology means that neither multi-stemmed nor single-stemmed plants are getting a head start on attracting pollinators by flowering and/or seed dispersal.

Although a previous studied overcompensation in terms of biomass (Belsky et al., 1993), our study focused on fitness measures. The total number of seeds was very similar in heads of multi-stemmed plants and single-stemmed plants. Although there were more filled seeds on average in heads of multi-stemmed plants, it was not enough to show a significant difference which means that multi-stemmed plants did not receive a much greater benefit from having more pollinators visiting their flowers and transferring pollen. However, the significant difference in reproductive success between multi-stemmed plants and single-stemmed plants shows that the advantage of multi-stemmed plants comes from having more heads containing seeds. The average number of filled seeds per plant in multi-stemmed plants was double that in single-stemmed plants. Since each head in both groups of plant contains a similar number of filled seeds, multi-stemmed plants having twice as many heads is the reason why they have a greater reproductive output. A greater seed output in multi-stemmed *C. pitcheri* equates to higher fitness and overcompensation in response to damage to the plant.

Further studies may need to be done in order to fully understand the reproductive success of *C. pitcheri*. Possible ideas for the future would be to focus more on pollinators and the reason why there are differences seen in number of potential pollinators and total pollination time. Since we found that there was not a significant difference in floral display between multi-stemmed and single-stemmed plants, regarding number of flowers per plant and flower size, there must be another factor to explain why multi-stemmed plants experience more pollination. If a study was done to observe the effect of distance to other flowering plants and its pollinators, I think we would see more potential pollinators due to a larger floral display. Another possible improvement to our study would be to observe these plants over an extended period of time. It is unknown whether *C. pitcheri* consistently exhibits overcompensation in response to herbivory. Perhaps there was a change in resources that affected the plants' growth and reproductive output. There is evidence of plants regrowing better when resources are abundant (Maschinski and Whitham, 1989) and also when resources are limited under stressful conditions (Rautio et al., 2005).

It remains unclear what the outcome of *C. pitcheri* will be in the future. If these plants exhibit overcompensation in response to damage including herbivory, it may be possible that there is a need for human intervention in order for the plants to increase its reproductive output. More studies gaining knowledge about this plant are required in the future to determine a solution to prevent this native thistle from becoming extinct. Perhaps this newly discovered information can be relevant to similar types of herbaceous species, which could change how we define "damage" to plants.

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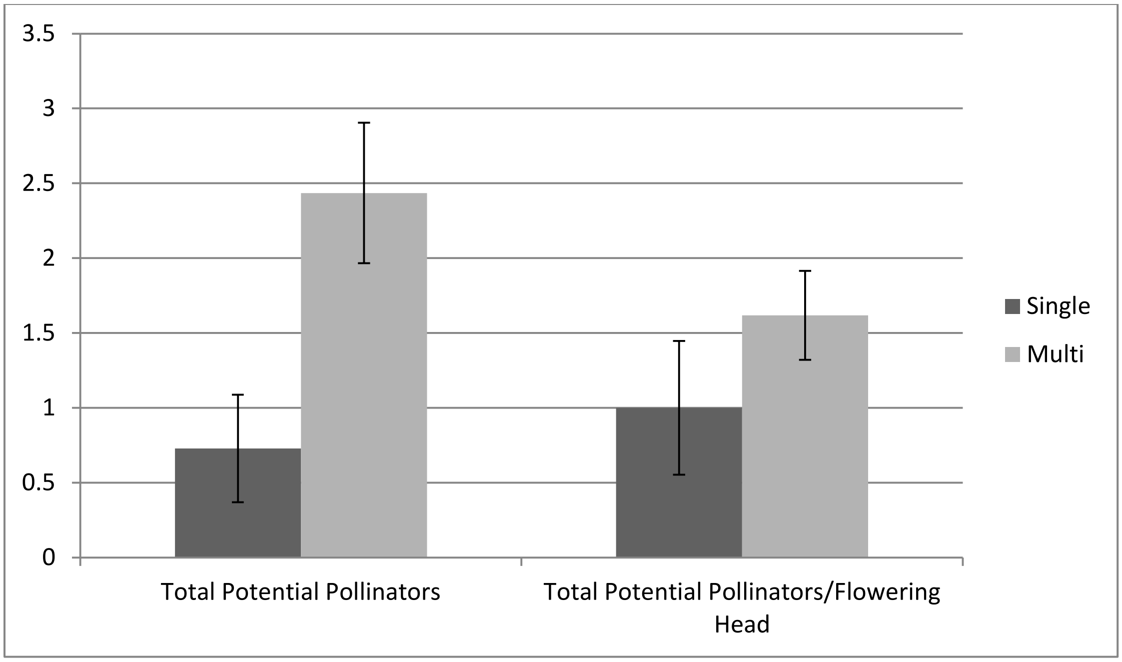

Figure 1. Histogram displaying the mean number of pollinators (p = 0.0035) and pollinators per flowering head (p = 0.145) between single-stemmed and multi-stemmed *C. pitcheri*

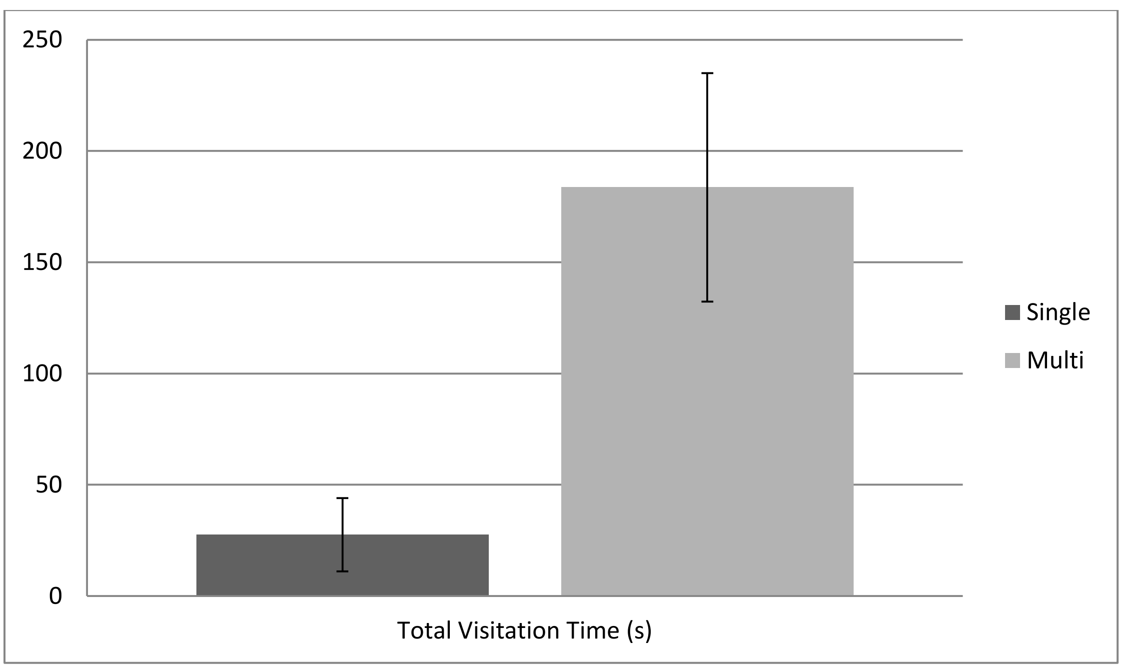

Figure 2. Histogram comparing total visitation time by pollinators in seconds between single-stemmed and multi-stemmed *C. pitcheri* (p = 0.004)

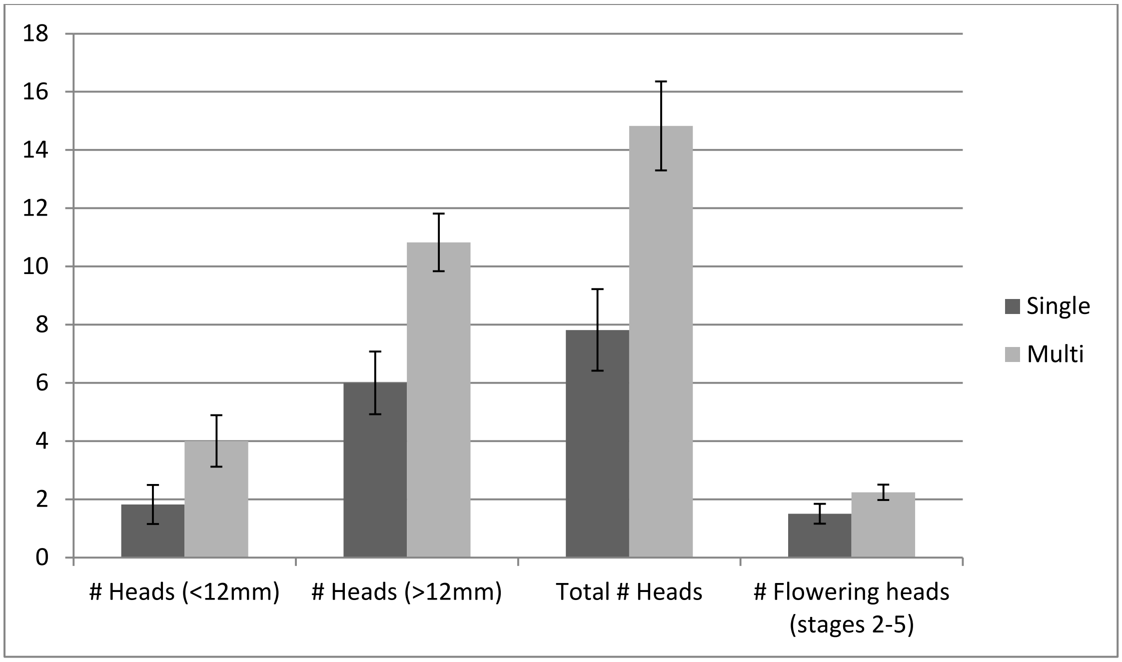

Figure 3. Histogram comparing number of heads <12mm ($p = 0.029$), number of heads >12mm ($p = 0.003$), total number of heads ($p = 0.0035$), and number of flowering heads ($p = 0.075$) between single-stemmed and multi-stemmed *C. pitcheri*

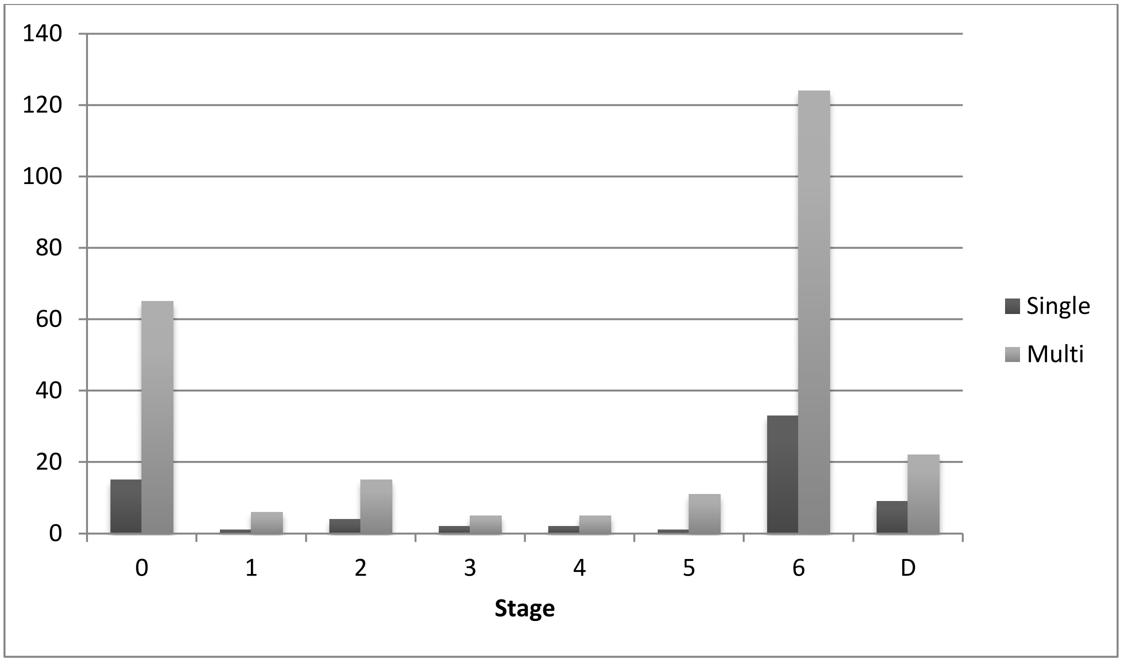

Figure 4. Histogram displaying the frequency of heads in stages 0-6 and dispersed in single-stemmed and multi-stemmed *C. pitcheri* ($p = 0.8$)

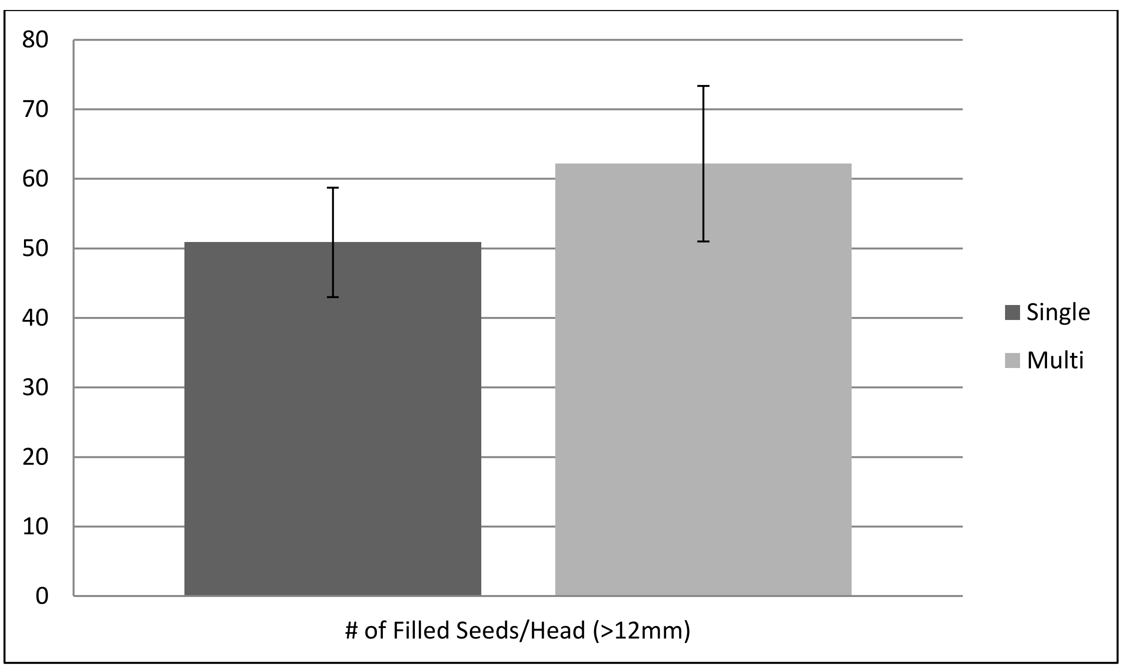

Figure 5. Histogram of number of filled seeds per head >12mm in single-stemmed and multi-stemmed *C. pitcheri* ($p = 0.118$)

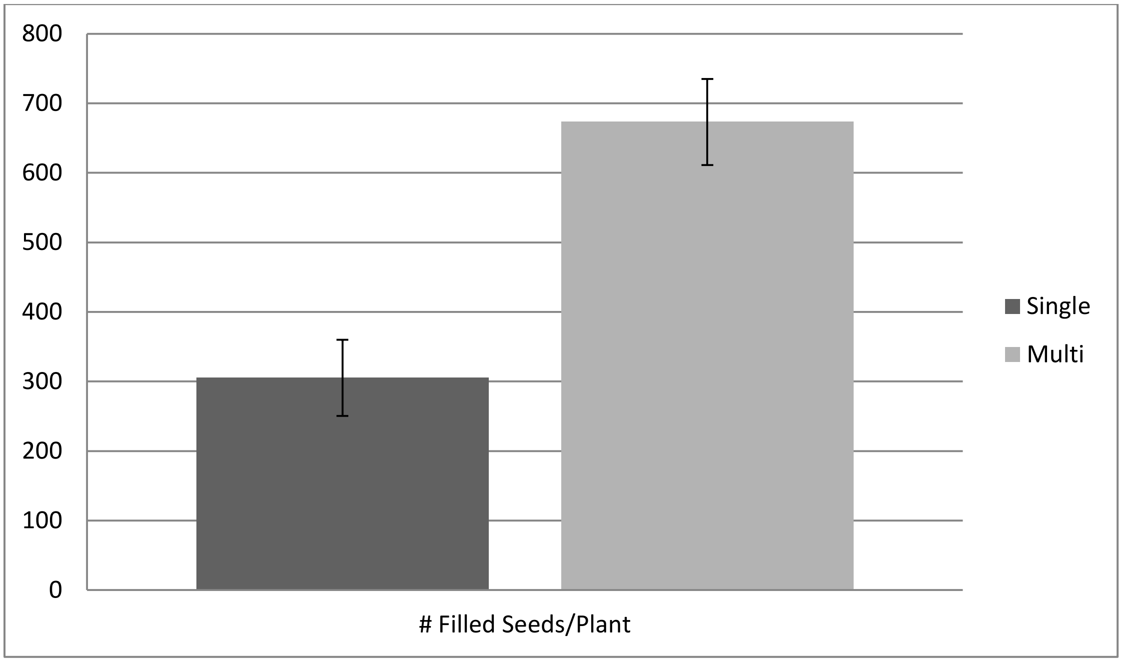

Figure 6. Histogram showing number of filled seeds per plant between single-stemmed and multi-stemmed *C. pitcheri* ($p < 0.001$)