GIGANTISM AS A PRODUCT OF SEXUAL SELECTION IN *SENECIO* SP.

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Abstract. Gigantism in herbaceous plants may be the product of pollinator-mediated sexual selection in areas where weather severely limits pollination time. Flowers of the gigantic herb, *Senecio* sp., at Cuerici Biological Reserve, Costa Rica, were used to test pollinator preference. Experimentally elevated inflorescences attracted a greater number of insect visitors than controls with similar floret numbers. Experimentally enlarged inflorescences also attracted more visitors than controls, but fewer visitors per floret. Pollinator preferences especially for increased height, may play a role in the evolution of gigantism in high altitude floral communities of the tropics.

INTRODUCTION

Cuerici Biological Reserve, Costa Rica, 3000 m above sea level, contains numerous anomolously large herbaceous plants, including at least two members of the Umbelliferaceae, along with a thistle and *Senecio* sp. from the Asteraceae. Occurring primarily in open field habitats, these plants reach heights of > 2 m with correspondingly large leaves and inflorescences. The repeated evolution of these gigantic plants at Cerro de la Muerte suggests a common environmental cause that has not been elucidated.

Insect visitations of *Senecio* sp. (including potential pollinators) tend to be concentrated during the midmorning hours, possibly because of the extreme diurnal temperature fluctuations that are characteristic of high altitude tropical environments. *Senecio* sp. and other pollinator-limited plants may have been under strong sexual selection to maximize pollination success during these limited hours of opportunity. We hypothesized that gigantism is a product of sexual selection mediated by pollinators that prefer higher inflorescences to lower inflorescences, and larger inflorescences to smaller inflorescences. We use the term "sexual selection" because we predict that the reproductive success of *Senecio* sp. has been increased by the evolution of gigantism even though this trait is not necessarily adaptive except for its affect on mating opportunities. We tested this hypothesis by experimentally manipulating inflorescence height and size, and monitoring the response of insect visitors.

METHODS

We studied *Senecio* plants in two fields at the Cuerici Biological Reserve, Costa Rica. We tested for effects of inflorescence height and size on potential pollinator visitation by manipulating *Senecio* plants in the field. Effects of inflorescence size were tested on 26 January 1996 (n = 4 replicates). Effects of inflorescence height were tested on 26 January (Trial 1, n = 5 replicates) and 27 January (Trial 2, n = 4 replicates).

Effects of inflorescence size were tested by cutting and doubling the natural inflorescence size. Size categories were: small (half natural inflorescence size, 15 cm at maximum diameter), control (naturally occurring size, ≈ 25 cm diameter), and large (double the natural inflorescence size, 45 cm). These manipulations involved cutting one inflorescence in half, leaving one at natural size, and combining two inflorescences. All three treatment classes were held at the same height.

Effects of inflorescence height were tested by raising and lowering inflorescences above and below natural height. Height categories were: low (1 m), control (naturally occurring height, ≈ 3 m), and high (4.1 m). Height manipulations involved tying down one inflorescence 1 m above ground, leaving one at natural height, and attaching one inflorescence on a pole at 4.1 m. Remaining plant inflorescences were left undisturbed in trial 1, but in trial 2 each experimental plant had only three inflorescences (at 1 m, 3 m, and 4.1 m). All inflorescences for height manipulations were approximately the same size.

We recorded numbers of insect visitors that were potential pollinators (contacted floral reproductive parts) between 0830 - 1130 on both days. Each replicated experimental array was monitored for 25 visits, or 30 minutes, whichever came first. Frequency of visitation to inflorescence treatments were compared using a Chi-square test. A nominal logistic regression (JMP Manual 1995) was used to test for between

plant effects within trials, and treatment effects between trials.

RESULTS

Height influenced visitor attraction in both height trials (Fig. 1; $X^2 = 40.41$, df = 2, $P < 0.005$ for trial 1; $X^2 = 39.88$, df = 2, $P < 0.005$ for trial 2). However, the two height trials differed ($X^2 = 9.92$, df = 2, $P < 0.01$). In height trial 1, when there were more inflorescences at the control height than at other heights, experimentally lowered inflorescences attracted the fewest insect visitors (≈ 10%), control inflorescences attracted the most (≈ 60%), and high inflorescences were intermediate (≈ 30%; Fig. 1). In the second height trial, when only the three experimental inflorescences were present, high inflorescences attracted ≈ 45% of the visitors, while both control and low attracted ≈ 28% each (Fig. 1). Replicated arrays within the height experiments did not differ in insect preferences ($X^2 = 22.52$, df = 14, $P > 0.05$), although variance among arrays was rather high in trial 2 (apparently due to wilting in some manipulated inflorescences).

Insect visitations also varied with inflorescence size (Fig. 2; $X^2 = 41.92$, df = 2, $P < 0.005$). Small inflorescences attracted only 3% of visitors, while control and experimentally enlarged inflorescences attracted ≈ 48% each (Fig. 2). Replicated arrays within the size experiments did not differ in visitor response ($X^2 = 0.49$, df = 6, $P = 0.99$). Assuming that an average visitor pollinates the same number of florets regardless of inflorescence size, insect visitation rates can be scaled by inflorescence area to approximate visits per floret. Given this assumption, visits per floret differed across inflorescence size ($X^2 = 34.78$, df = 2, $P < 0.001$), with control inflorescences attracting the greatest number of visitors per floret, large attracting 34% as many, and small attracting only 19% as many visitors per floret as control inflorescences.

DISCUSSION

Results support the hypothesis that gigantism in *Senecio* sp. at Cerro de la Muerte is a product of sexual selection mediated by pollinators. Pollinators preferred higher inflorescences over lower ones and larger inflorescences over smaller ones. Both size and height appear to work together in attracting pollinators. In the treatment with one inflorescence sticking above and one below the bulk of the plant inflorescences, the pollinators vistied the control most

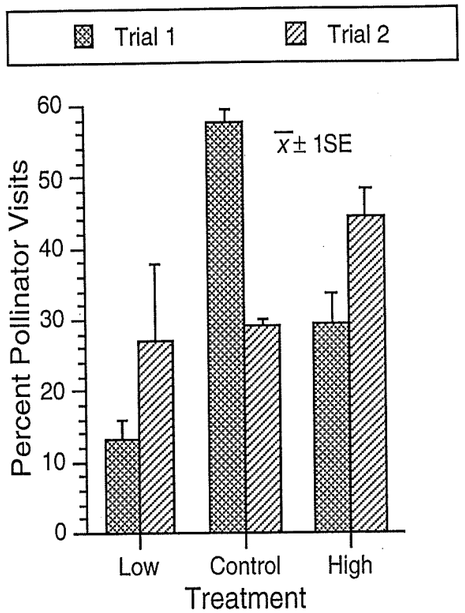

Figure 1: Preperences of insect visitors for *Senecio* inflorescences at three heights (n = 5 and 4 replicates for trials 1 and 2 with a total of 132 and 101 insect visitors, respectively).

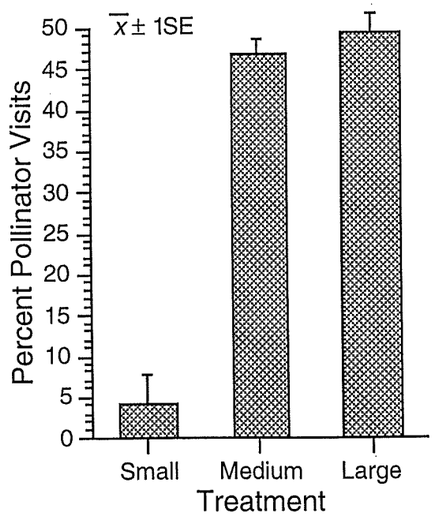

Figure 2: Preference of insect visitors for *Senecio* inflorescences at three heights (n = 4 replicate arrays with a total of 101 insect visitors).

frequently. When all other inflorescences were eliminated, the pollinators visited the higher inflorescences more. Thus, size (in this case the majority of the inflorescences on the plant) and height are interrelated, and perhaps both contribute to reproductive strategy for *Senecio*.

Results suggest that contemporary selection is not favoring further increases in inflorescence size because larger inflorescences did not receive enough additional insect visitors to balance the larger number of florets that require pollination. Instead, inflorescence size appears to currently be under stabilizing selection. This conclusion assumes that each insect visitor pollinated an equal number of florets per visit, irrespective of inflorescence size. If instead, average visitors stay longer and pollinate more florets in larger inflorescences, then selection might be favoring further increases in inflorescence size. Future studies are required to discriminate among these alternative interpretations.

Our sexual selection hypothesis was supported, but alternative hypotheses remain. The sexual selection hypothesis as we have developed it would be weakened by finding cases of gigantism in plants that are wind pollinated. *Alnus*, a wind-pollinated giant also found at Cuerici Biological Reserve, might be an example of gigantism selected for through a mechanism other than sexual selection. In addition, *Senecio* sp. is wind dispersed and a higher inflorescence might have higher dispersal success. It is possible that wind dispersal and pollinator preference are working in conjunction to select for larger plants. This hypothesis would be weakened by examples of gigantism in species that employ biotic seed dispersal agents. Gigantism may also be a result of abiotic conditions unique to Cerro de la Muerte such as increased soil nutrients or light availability. Finally, it is possible that gigantism is not the result of selection, but rather a neutral trait that has persisted through time.

Although sexual selection mediated by pollinators may be a mechanism by which *Senecio* sp. has evolved, it would be interesting to examine the distribution of other giants with respect to potential pollinator limitations. Clearly, pollinator limitation by itself does not necessarily lead to gigantism, as in the Arctic tundra where pollinator limitations are frequent but plant stature is greatly reduced. Our study suggests that sexual selection via insect visitation choices may lead to gigantism in the Costa Rican cerro, but gigantism can still evolve in suitable abiotic environments.

Literature Cited

JMP Statistics and Graphics Guide. Version 3.1. Cary, NC: SAS Institute, Inc., 1995.