Sexual selection or wind dispersal? Alternative explanations for the evolution of gigantism in *Dahlia species* (Asteraceae)

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Abstract

Several species of herbaceous plants located at Cuerici Biological Reserve, Costa Rica, grow to an unusually large size relative to confamilial species. Lief et al. (1996) provided evidence that this gigantism was due to sexual selection (mediated by pollination) for large, high inflorescences (clusters of flowers). An alternative hypothesis maybe that gigantism is a product of selection for increased seed dispersal distance. We tested these hypotheses with studies of Dahlia sp., an unusually large species of the Asteraceae. Pollinator visitation rates, but not seed set, were greater in high inflorescences compared with low inflorescences. However, winged seeds released from 4 m traveled 5 m farther, on average, than seeds released from 2 m (4 m and 2 m are representative heights of tall and short flowers). This difference in dispersal distance seems large enough to be biologically meaningful because seeds dispersed from 4 m would commonly escape the proximity of adult plants while seeds dispersed from 2 m would not. Therefore, enhanced seed dispersal is one advantage of increased height in Dahlia sp. The seed dispersal hypothesis, however, does not easily explain the prevalence of gigantic herbs in the high altitude tropics. Additional selection pressures introduced by an unusually high nutrient availability that permits rapid, vegetative growth in these ecosystems may also have contributed to the evolution of gigantic herbs.

INTRODUCTION

Adaptations to extreme environments can often lead to convergent evolution. This phenomenon can be observed at the Cuerici Biological Reserve, Costa Rica, where numerous, unrelated herbaceous plant species grow to unusually large sizes (i.e., large relative to confamilial species in other areas). This trend towards gigantism seems to be common in high altitude tropical ecosystems. Lief et al. (1996) provided experimental evidence that sexual selection, mediated by pollinator preference, has favored individuals of Senecio species (Asteraceae) that present their flowers at the greatest heights. However, height may also be advantageous for purposes other than pollination. Several of the gigantic species found at Cuerici have wind dispersed seeds (e.g., *Circium sp.*, *Senecio sp.*, and *Dahlia sp.*) and height may be an adaptation to aid in seed dispersal. In general, objects that are aerodynamically suited to fly, such as wind dispersed seeds, are likely to travel farther horizontal distances when released from greater heights. Whether or not this distance is biologically meaningful depends on the ecology of the species and the environment, but it is generally assumed that seeds that germinate further from a parent plants have higher survival (Janzen, 1970).

Dahlia sp. is a very large member of the Asteraceae family, with inflorescences that contain approximately 100 flowers and are insect pollinated. Each fertilized female flower develops one winged, wind-dispersed seed. Flowering is staggered among individuals, so flowering and fruiting tend to occur simultaneously within a population. We explored both the sexual selection and seed dispersal hypotheses for gigantism in *Dahlia sp.* If sexual selection drives *Dahlia sp.* gigantism, then pollinators should visit high flowers at a greater frequency than low flowers, and a greater proportion of seeds should be found in the fruiting bodies of taller plants. If enhanced seed dispersal has favored gigantism, then seeds dropped from a greater height should disperse substantially further than seeds dropped from a lower height.

METHODS

We recorded the number of pollinator visits to inflorescences of seven haphazardly-selected individuals of *Dahlia sp.* representing each of two height classes (high: ≥ 4 m; low: ≤ 3 m). This was repeated at each of seven observation stations along the road east of the Cuerici Biological Field Station (thus, total n = 49 high inflorescences and 49 low inflorescences).

Observation periods lasted 30 min. and took place between 09:00 - 12:00 on 29 January 2000. Chi–square analyses were used to test for effects of flower height on the number of individual insects that visited and the total number of visits to flowers (some individual insects visited more than one flower in the patch). The mean number of visitations per pollinator for high and low flowers was compared using a Student's t-test.

To investigate the relationship between flower height and seed production of *Dahlia sp.*, we sampled a single, closed, inflorescence from 10 plants in each of 2 size classes (high ≥ 4 m; low ≤ 3 m) and recorded the total number of seeds and wings per inflorescence. Preliminary studies also showed that not all flowers set seed, therefore we estimated the proportion of pollinated female flowers in each inflorescence by dividing the number of seeds by the number of wings in each fruit. A Student's t-test was used to compare the proportion seed set of high vs. low fruits.

To test the seed dispersal hypothesis, we first measured the heights of 20 fruiting *Dahlia sp.* to quantify the natural height range for the species (2.0 – 6.5 m). The frequency distribution of heights showed two modes, one near 2 m and another near 4 m, so we chose these as heights for seed dispersal measurements. We released 50 seeds from each height, and recorded their horizontal dispersal distance. Wind speeds were < 5 mph during all trials. The 4 m release point, accessed by climbing a tree, was directly above the 2 m release point. The dispersal area was relatively free from obstructing vegetation and each seed was untouched from release to contact with the ground. Seed dispersal distances were log-transformed and the averages were compared using a Student's t–test. We also compared the frequency distributions of dispersal distances from each height.

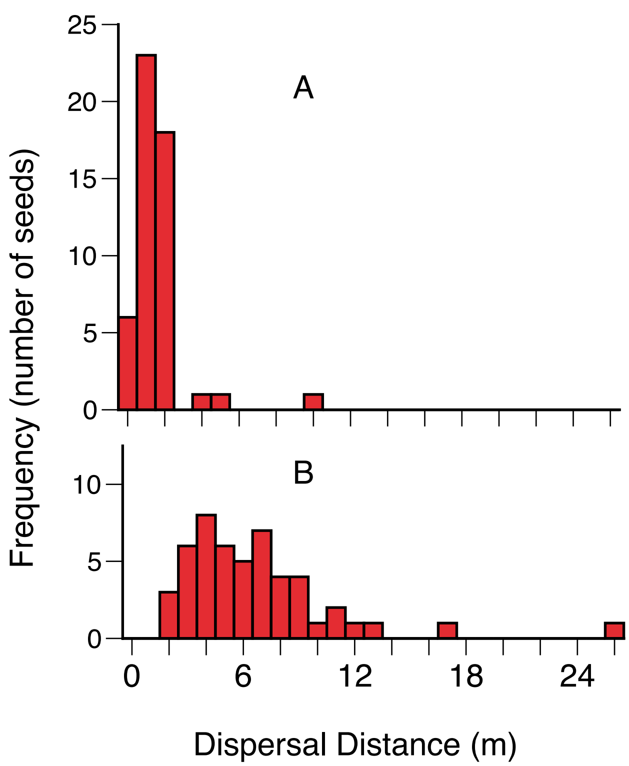

Figure 1. Frequency distributions of dispersal distances of *Dahlia sp.* seeds released from 2m (**A**) and 4m (**B**).

RESULTS

During pollinator observations, *Dahlia sp.* inflorescences were visited by Bombus sp., an unidentified small bee species, and an unidentified hummingbird species. The hummingbirds fed on the nectar but did not appear to contact the stigmas or anthers, so were excluded from analyses of pollinator visitations. High flowers had a greater total number of visits than low flowers (38 vs. 22, respectively; chi-square = 4.27, df = 1, P = 0.04), but there was no significant difference in total number of pollinating individuals (17 high vs. 12 low; chi-square = 1.69, df = 1, P = 0.19), or number of visits per pollinating individual between high and low flower heights, (mean ± SE = 2.1 ± 0.39 and 1.8 ± 0.46 for high and low, respectively; t = 0.46, df = 28, p = 0.65, respectively).

The proportion of flowers (mean ± SE) that produced apparently viable seeds was not different between high and low fruit heights (0.33 ± 0.05 and 0.46 ± 0.05 respectively; t= 1.58, df = 15, p = 0.14). Absolute numbers of seeds (mean ± SE) in each inflorescence were also not different between high and low fruits (37.6 ± 7.1 and 55.2 ± 6.8, respectively; F1,18 = 1.80, p = 0.09). Average dispersal distance and the range in dispersal distance were both significantly greater for seeds released from 4 m vs. 2 m: mean ± SE = 6.61 ± 4.10 m vs. 1.57 ± 1.46 m; t = 12.05, df = 98, p < 0.0001; range = 1.8 – 25.7 m vs. 0.2 – 9.5 m (Fig. 1).

DISCUSSION

Although we found that high flowers were visited more often than low flowers, seed set did not differ between the two heights. This suggests that high and low flowers are equally pollinator-limited, and therefore more frequent pollinator visitation confers relatively little benefit to recruitment in *Dahlia sp.* Our observations of pollinator visitation are consistent with the findings from Lief et al. (1996), but if higher insect visitation does not lead to higher seed set, there is no obvious fitness benefit, and the evolution of gigantism requires a different explanation than sexual selection for higher inflorescences.

Our dispersal measurements clearly show that seeds disperse farther from tall plants than from short plants. The greater dispersal distance attributable to taller height (Fig. 1) could increase plant fitness through reduction in juvenile predation, parasitism, and competition for nutrients and light with established conspecifics and other neighbors (Janzen, 1970). *Dahlia sp.* tend to grow in patches that are 0.5 – 10 m in diameter. The mean difference in dispersal distance between high and low treatments (5 m) would often be far enough to carry a seed beyond a dense stand of conspecifics, and is therefore likely to be biologically meaningful. One problem with the seed dispersal hypothesis is that it seems these benefits should apply equally well in any environment, so it remains unclear why gigantism should be a unique feature of tropical high altitudes.

Other factors may have influenced the evolution of gigantism in *Dahlia sp.* For example, it may be an adaptation to intense competition for light or a result of abiotic conditions unique to high-elevation tropical ecosystems. The soil at Cuerici is relatively young, derived from recently deposited volcanic rock and marine sediments, and is probably quite fertile for a tropical ecosystem (Castillo-Munoz 1983). The size distribution of *Dahlia sp.* at Cuerici suggests that plants grow up to 2 m per year, which seems rapid relative to similar species in other environments. This is consistent with the hypothesis that a favorable abiotic environment has contributed to the evolution of gigantic herbs. Although the evolution of this striking feature of the high altitude tropics cannot yet fully be explained, it seems likely that seed dispersal and the abiotic environment play a role in the development of this trait.

REFERENCES

Castillo-Munoz, R. (1983). Geology. In D. H. Janzen (Ed.), *Costa Rican natural history* (pp. 41-67). Chicago, IL: University of Chicago Press.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104, 501-528.

Lief, G. M., Kopplin, S. E., Rutherford, A. C., & Shumate, A. M. (1996). Gigantism as a product of sexual selection in *Senecio sp.*. In A. L. Mannan & D. S. Canny (Eds.), *Dartmouth studies in tropical ecology* (pp. 62-64). Dartmouth College, Hanover, NH.

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