BRACT MORPHOLOGY AS A DEFENSE AGAINST HERBIVORY IN HELICONIACEAE AND MARANTACEAE

KYTJA E. WEIR AND ERIN A. WRIGHT

Abstract. Water in the erect bracts of *Heliconia* inflorescences (Heliconiaceae) may protect developing flowers and fruits from terrestrial herbivores. *Calathea lutea* (Marantaceae) has similar bract morphology and also usually contains water in its bracts. We hypothesized that the presence of water in both Heliconia and Marantaceae bracts would reduce herbivory to reproductive flower parts. Due to unusually dry weather in Corcovado National Park, water stressed inflorescences no longer contained water in some areas. Comparison of inflorescence damage across mesic and arid habitats indicated that dry bracts of *Heliconia latispatha* had higher rates of herbivory than water-filled bracts. *C. lutea* did not exhibit differential herbivory damage between sites, suggesting that water-filled bracts in *C. lutea* serve a different function than in Heliconia despite their convergent morphology.

Key Words: Calathea lutea, *convergent morphology,* Heliconia latispatha, Heliconia wagneriana

INTRODUCTION

Many plants have intricate systems of herbivore defense, from chemicals such as tannins to morphological adaptations such as spines. It has been suggested that *Heliconia* floral morphology (Heliconiaceae), in which flowers mature in water-filled, cuplike bracts, evolved as a mechanism to reduce herbivory to reproductive parts by terrestrial insects (Seifert 1982). An unusually dry February in Corcovado National Park left many heliconia bracts dry, providing an opportunity to test this hypothesis. Normally at this time of year, bracts in the vicinity of Sirena Estacion Biologica contain water (Barnhorst et al. 1995; Bird and Jackson, 1996; M. P. Ayres, pers. comm.). The convergent morphology of Marantaceae inflorescences, which are also a series of water-filled bracts, suggests that the herbivory defense hypothesis may also apply to *Calathea lutea*, a common species of Marantaceae at Corcovado.

We examined floral herbivory, bract water content, and soil water availability in *Heliconia wagneriana, Heliconia latispatha,* and *C. lutea.* The herbivory defense hypothesis predicted more herbivory damage in *H. wagneriana, H. latispatha,* and *C. lutea* inflorescences found in areas of lower soil moisture.

METHODS

We collected inflorescences of *H. latispatha, H. wagneriana,* and *C. lutea* in a mesic and an arid site on 5-7 February 1998 in Corcovado National Park, Osa Peninsula, Costa Rica. The mesic site was located on the bank of the Rio Pavo, 25 m downstream of the Sendero Pavo. The arid site was a small field on the Sendero Rio Claro ≈ 200 m from the field station.

At each site we measured soil moisture, haphazardly chose a sample of inflorescences for each of the three species, and quantified herbivory. For *C. lutea,* we measured the percent of bracts in each inflorescence with visible herbivory damage to the reproductive parts (n = 9 and 10 inflorescences at the mesic and arid sites, respectively). For *H. latispatha* and *H. wagneriana,* sample size was limited by the availability of inflorescences in the mesic site (n = 3 and 10 inflorescences of *H. latispatha* at mesic and arid sites; n = 5 inflorescences of *H. wagneriana* at the arid site). We found *H. wagneriana* inflorescences at three additional sites (two sites on Sendero Pavo, ≈3 and ≈15 km NW of Sirena Estacion Biologica, and one site on the Sendero Rio Claro, ≈200 m upstream from the estuary), although none could be included in our sampling due to time constraints.

Heliconia inflorescences exhibit successional maturation from base to top bracts, with each bract containing < 16 flowers or fruits in various developmental stages. We quantified herbivory damage as the percent of flowers damaged by herbivory in each of the top four open bracts of each inflorescence. For all *Heliconia* and *C. lutea* bracts, we measured the ratio of water depth to bract depth as an index of water content.

We used correlation analysis to compare bract water content and soil moisture. We analyzed the effect of site on herbivory in *C. lutea* with a one-way ANOVA. We analyzed herbivory in *H. latispatha* with a nested ANOVA that tested for effects of patch and variation among inflorescences within patches (with patches and plants treated as random effects). We analyzed the heliconia data from arid sites using two-way ANOVAs that tested for effects of bract position, inflorescence, and the interaction between bract position and inflorescence. All proportional data were arcsin transformed. Figures show non-transformed data.

RESULTS

Soil moisture varied between the two sites (mean ± SE = 29.5 ± 3.1% vs. 0.0 ± 0.0% for mesic and arid sites, respectively). None of the bracts in the arid site contained quantifiable moisture. In the mesic site, *C. lutea* bracts were more than half-filled with water (mean ± SE = 59.5 ± 3.7%). The only *H. latispatha* inflorescence containing water was filled to ≈ 65% (± 6%) capacity. Within the mesic site, soil moisture was positively correlated with bract water content in *C. lutea* (Spearman rho = 0.85; P < 0.001).

Within bracts, we found several species of beetles, mites, syrphid fly larvae, and other maggots. Presumably, some or all of them were responsible for feeding damage to the reproductive parts. For *H. latispatha,* there was more damage to reproductive flower parts in bracts per inflorescence in the arid site than in the mesic site ($F_{1,11}$ = 2.95; P= 0.006; Fig. 1). In *C. lutea,* however, damage from herbivory did not vary between arid and mesic sites ($F_{1,17}$ = 0.06; P= 0.95; Fig. 1).

Within heliconia inflorescences, the amount of herbivory varied with position of bracts. In the arid site, the newest bracts exhibited less damage than older bracts in both *H. latispatha* and *H. wagneriana* inflorescences (*H. latispatha* : $F_{1,9}$ = 18.6; P < 0.001; *H. wagneriana*: $F_{1,4}$ = 6.33; P= 0.03; Fig. 2). Within the arid site, *H. latispatha* had little variation in herbivory among inflorescences ($F_{1,9}$ =1.59; P = 0.19) and no interaction between bract position and inflorescence ($F_{1,9}$ = 0.74; P = 0.67). In contrast, there was significant variation among inflorescences in *H. wagneriana* ($F_{1,4}$ = 10.10; P < 0.01), but again, there was no interaction between inflorescence and bract position ($F_{1,4}$ = 2.64; P = 0.097).

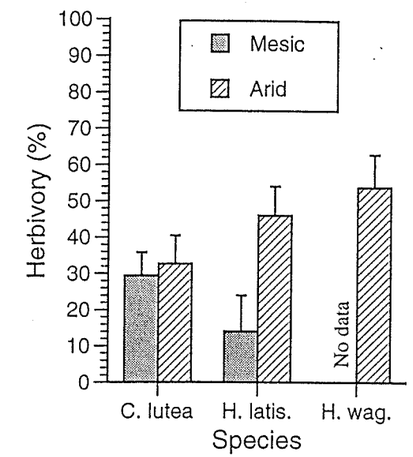

FIG. 1. Damage from herbivory in reproductive parts of *Calathea lutea, H. latispatha, and H. wagneriana* in arid and wet sites.

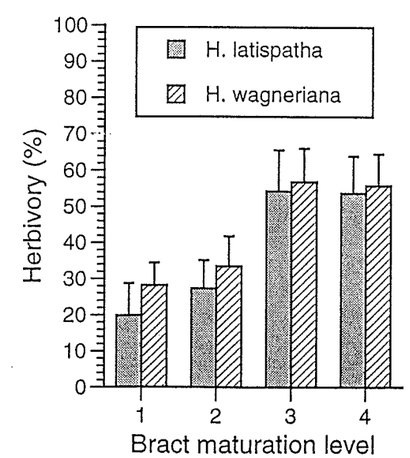

FIG. 2. Effect of bract position (1 = newest) on herbivory damage to reproductive parts in *Heliconia spp.* inflorescences.

DISCUSSION

Heliconia flower morphology appears to serve as a mechanism for reducing floral herbivory. *H. latispatha* inflorescences in the arid sites had three times more herbivory damage to their bracts than plants in the mesic site. Although few Heliconia inflorescences contained water at the time of our measurements, higher soil moisture at the mesic site and more water in the *C. lutea* bracts suggest that Heliconia bracts at the mesic site contained water more recently than those in the arid site. Presumably, the patterns in herbivory that we recorded were the result of herbivory that partly occurred before the bracts were dried out. The benefits incurred by the plant from reducing herbivory of reproductive plant parts must outweigh the cost of actively transporting water to keep the bracts full, even when water resources are quite low.

The amount of herbivory damage to *C. lutea* inflorescences did not differ between the arid and the mesic sites, despite the difference in bract water content between the two sites. It could be that although inflorescences of Heliconiaceae and Marantaceae have similar morphology, the water-filled bracts in Marantaceae require a different explanation than herbivore defense. For example, the water in the bracts, possibly sweetened with glucose or containing insects, might serve as an attractant to insects or birds who pollinate the flower in the process of visiting the bract, but this seems unlikely given the positioning of the flower as it emerges from the bract. The slightly viscuous water solution might serve to protect the flowers from desiccation during development (R. Rojas, pers. comm.), or perhaps the water-filled bracts of the Marantaceae are an anachronism from selection by some now extinct herbivore.

Alternatively, water-filled bracts in the Marantaceae may reduce floral herbivory, but we may have been unable to detect the response because their bracts only recently dried up. We cannot assess exactly when these bracts dried up nor when herbivory occurred. Given that most *H. latispatha* bracts in the mesic site were dry, whereas *C. lutea* bracts still contained water, it must be that *C. lutea* had greater water reserves (perhaps due to deeper roots) or were allocating more of their water to the bracts. If bract water is an anti-herbivore defense in *C. lutea*, sampling later in the dry season, or across a steeper gradient in soil moisture, should yield differences in herbivory damage.

LITERATURE CITED

Barnhorst, A. V. and N. C. Pouliot. 1995. The aquatic invertebrate communities of three species of plants with bract flowers. Pp. 84-86 *in* C. D. Wray, editor. Dartmouth Studies in Tropical Ecology, Hanover, NH, USA.

Bird, S. P. and C. D. R. Jackson. 1996. Processing chain interactions between detrivourous insect populations in *Heliconia wagneriana*. Pp. 89-92 *in* A. L. Mannan and D. S. Canny, editors. Dartmouth Studies in Tropical Ecology, Hanover, NH, USA.

Seifert, R. P. 1982. "Neotropical Heliconia Insect Communities." *The Quarterly Review of Biology* 57(1): 1-28.