THE ADAPTIVE NATURE OF FLORAL BRACTS IN FOUR *HELICONIA SPP.*

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Abstract: Inflorescences of *Heliconia spp.* include those that hang down from the stem (pendant), and those that have cup-like bracts filled with fluid (upright). These traits appear to be homoplastic, having evolved several times in different clades. We explored the potential benefits of upright bracts, hypothesizing that liquid in the bracts would reduce herbivory levels on the flowers, and/or prevent nectar-robbing mites from entering the flowers. In fact herbivory was lower in *Heliconia spp.* that had upright bracts. We also found a significant difference in herbivory levels between the two upright species, *H. imbricata* and *H. wagnerania*. Our tests for mite colonization of drained flowers were inconclusive because none of the manipulated flowers bloomed during our study. The multiple ecological processes probably contribute to the diversity of flowering plants.

Key words: Heliconia imbricata, Heliconia mariae, Heliconia pogonantha, Heliconia wagnerania, *herbivory, inflorescence, La Selva, orientation, phoretic mites*

INTRODUCTION

Flowering plants (Division: Anthophyta) are the largest and most successful plant group on earth today. The success of this group can be attributed in part to the diversity of structure and function in the reproductive organ, the flower itself. Clearly, the evolutionary diversification of flower structure has facilitated the diversification of flowering plants in habitats of all types (Heywood 1993).

Members of the genus *Heliconia* (Heliconiaceae: Zingibierales) are large-leaf herbs found throughout the neotropics. The floral parts of a plant are positioned within a bract, which are located in series on an inflorescence. Several species have inflorescences of pendant orientation with respect to point of attachment to the stem (e.g., *H. pogonantha*), while others (e.g., *H. wagneriana*) have upright inflorescences. The species exhibiting upright inflorescences often have unusual cup-like floral bracts that contain liquid, commonly thought to contain plant secretions. These bracts typically sustain surprisingly diverse communities of aquatic (or semi-aquatic) insects (Seifert 1980).

Phylogenetic analyses indicate that the upright inflorescence is the primitive state in *Heliconia*, and that the pendant state has independently evolved twice (Kress 1981). The same analysis, however, also indicated that upright bract orientation is a homoplastic trait as well, having evolved again from the pendant state. Such reversals make it reasonable to hypothesize that the current state of any species (upright vs. pendant) is a product of contemporary selection rather than an evolutionary anachronism.

Several hypotheses have been developed to explain the benefits of having an upright bract. Skutch (1933) was the first to suggest that the water-filled bracts served to prevent attacks from terrestrial insects and larvae that feed on flowers and flower parts. The flowers remain submerged until they are ready to be pollinated, and are therefore protected from herbivory by terrestrial insects. The bract liquid may also prevent hummingbird associated nectar-robbing mites from entering the flower. It seems that *H. wagneriana* at La Selva does not support a mite population below the top inflorescence (McDade, pers. comm., Hellmuth, pers. obs.). Two species of mite-carrying hummingbird visitors (*Phaithornis superciliosus* and *Glaucis aenea*) commonly visit *H. wagneriana* flowers. However, because the flowers remain sub-

merged until ready to pollinate, and then often senesce quickly to fall back into the liquid, mites may be selectively avoiding the upright *Heliconia* species. Top inflorescences may host mites because of the low volume of liquid.

To identify the benefit of having an upright orientation, we compared the occurrence of herbivory of two upright species (*H. wagneriana* and *H. imbricate*) and two pendant species (*H. mariae* and *H. pogonantha*). Both upright species hold water in their bracts that harbors a diverse invertebrate community, whereas the pendant species contained no water or aquatic invertebrates. Additionally, we tested whether the presence of bract water influenced the absence of mites in *H. wagneriana*.

METHODS

On 15 - 16 February 2004, we compared floral herbivory on two upright species (*H. wagneriana* and *H. imbricata*) and two pendant species (*H. pogonantha* and *H. mariae*). Inflorescences were collected from areas surrounding the OTS field station at La Selva National Park, Costa Rica. We located three distinct patches of each species along the SAZ trail, and sampled one inflorescence from each patch. On each inflorescence from each species, we quantified the herbivory levels on the top, middle and bottom flowers of each inflorescence (to partition variance due to flower age). We recorded the presence or absence of herbivory on the petals, seeds, and inside of the bracts of each flower. Herbivory on the inside of the bract was only recorded if it covered > 5% of the surface area. We used a chi-square test to compare the probability of herbivory on reproductive floral structures, on non-reproductive floral structures, and overall herbivory, between pendant and upright inflorescences, as well as between species within a bract type.

We also tested the effect of bract liquid on the colonization of mites on flower parts of *Heliconia wagneriana*. We did this by comparing mite abundance between drained bracts and intact bracts. On 14 February 2004, we used a dissection knife to slice 1 x 1 cm holes into the bases of the bracts of 140 flowers on 23 inflorescences in three different *H. wagnerania* patches located on the SAZ trail. We were careful to avoid damage to interior flower parts. For the next three days we checked each drained bract and neighboring intact bract for flowering, hummingbird visitation, and mites.

RESULTS

Bract orientation and species within bract orientation were related to herbivory intensity on both reproductive and non-reproductive tissue (Table 1). Bracts of the pendant inflorescences were more likely to have herbivory on the reproductive parts than bracts on upright inflo-

Table 1. The percent of *Heliconia* bracts with herbivory on the inside of the container bract, on the petals, or on the internal reproductive parts (stamen, pistil, ovary, or seeds).

Inflorescence type	Species	Bract herbivory (inside)	Petal herbivory	Reproductive herbivory
Upright	*H. imbricata*	88	77	44
	H. wagneriana	0	22	0
Pendant	*H. mariae*	11	33	44
	H. pogonantha	0	77	66

rescences (χ^2 = 4.21, df = 1, P = 0.04); however, herbivory on the non-reproductive parts, and overall herbivory was not different between bract orientations (χ^2 < 0.001, df = 1, P = 0.99 and χ^2 = 2.6, df = 1, P = 0.11, respectively). Within the upright floral structure type, *H. imbricate* had more herbivory on both reproductive (χ^2 = 5.14, df = 1, P = 0.02) and non-reproductive structures (χ^2 = 8.10, df = 1, P < 0.01) than *H. wagneriana*. There was no difference in the occurrence of herbivory between the two pendant species (reproductive, χ^2 = 0.90, df = 1, P = 0.34; non-reproductive, χ^2 = 1.60, df = 1, P = 0.21).

Unfortunately, none of the experimentally drained bracts or their undrained controls flowered during the experiment. Consequently, there was no hummingbird visitation, and no opportunity to evaluate whether mites associated with the hummingbirds were more likely to colonize drained flowers.

Discussion

Heliconia spp. with upright bracts sustained less flower herbivory than those with pendant bracts, which is consistent with the hypothesis that upright bracts have been selected for in *Heliconia* because the fluid retained within bracts protects reproductive parts. Pendant inflorescences, however, are not the ancestral condition of these plants, suggesting it too is an adaptation and implying that there must also be factors that can favor pendant bracts in *Heliconia* flowers. One possibility is that although upright bracts limit herbivory on the flowers by terrestrial insects, they expose the plant to potential aquatic herbivores (Seifert 1982). Additionally, it is possible that the pendant inflorescences evolved as an adaptation to increase pollination events (Seifert 1982).

We also found a significant difference in herbivory levels between the two upright species, *H. imbricata* and *H. wagnerania*. It has been suggested that the chemical composition of the fluid may mediate the structure of the aquatic (or semi-aquatic) community that is harbored in the bract (Bronstein 1986). The plant can regulate several aspects of the bract fluid, including the pH (Butcher 2002) and sugar concentration (Nutter 2000), which may then influence the composition and abundance of the community (e.g., eliminating aquatic herbivores). Further studies could compare the pH of the liquid and the aquatic communities found in the bracts of these two species to determine there is any relationship.

We were unable to evaluate the hypothesis that upright bracts protect flowers against nectar theft by mites associated with hummingbirds. Field observations revealed that mites are commonly found in top inflorescences, which hold a very small volume of water compared to the bracts that were lower down on the inflorescence. Furthermore, a pilot study on a single plant revealed that two bracts that were drained (and which subsequently bloomed) were both colonized by mites. Mites are selective in their choice of plants to colonize, sometimes avoiding entire families of plants such as the *Acanthaceae* (McDade, pers. comm.). It is possible that the mites have evolved a mechanism that prevents them from colonizing *H. wagnerania*; these flowers only bloom for a single day before falling back into the water, giving the mites little time to escape from the flower after feeding on nectar. Future studies could examine what cues the mites use in the decision of which flowers to colonize.

Our study indicates that herbivory is one selective pressure that influences the bract type of *Heliconia* flowers. It is likely that pendant inflorescences are associated with other advantages since they have evolved at least twice in this genus. Apparently, there are multiple ecological processes, involving numerous other organisms that influence the evolution of floral

morphology in *Heliconia*. This range of selective pressures influencing the evolution of flower structure in flowering plants is likely responsible for a large part of the diversity and success of the group as a whole.

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