of outcrossing for reproductive success. In addition, the high variation in nectar production among individual flowers may represent a mechanism to encourage pollinators to move from one vine to the next. Resolving this spatial variation would likely cast more light on the nocturnal flowering and pollination biology of *Ipomoea*.

Literature Cited

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NECTAR ROBBERY: COMMUNITY CRIME PREVENTION

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Abstract. We assessed floral morphology in sun- and shade-adapted species to test the hypothesis that plants should optimally allocate resources to nectar defense. Greater defense in sunny habitats may be a response to increased visitations by potential robbers. Differences in defense between habitats were small compared to the morphological variety between species within habitats. This suggests that nectar robbery exerts relatively little influence on floral evolution.

Key Words: flower morphology, mutualism, nectar robbery, pollination syndrome

Introduction

Flower morphology frequently offers clues about the evolution of mutualisms between flowers and their pollinators. Flower morphology might be affected not only by pollinators, but also by interspecific competition and the need for defense against nectar robbery. Nectar robbers are usually insects or birds that feed on a flower's nectar without touching the reproductive organs. To the extent that nectar production requires energy, this loss of nectar without any possibility of pollination represents a loss of resources and therefore a potential decrease in fitness. To reduce these costs, flowers may develop morphologies that either limit the access of potential robbers to nectar, or make it harder for them to avoid contact with the reproductive organs.

The cost of nectar robbery is simply the carbon cost of continuously replenishing the nectar supply. In addition to the nitrogen and carbon costs of producing new plant tissue for defense structures, defensive morphologies may have reproductive costs. By altering flower morphology to limit access of nectar robbers, a plant may also reduce its accessibility to certain pollinators and possibly decrease its pollination success. If a plant moves the anther closer to the nectar tube hole so that it is difficult for a robber to avoid contact with the reproductive organs, there is an increased risk of wasting pollen by mis-targeting an ineffective pollinator, or diluting the amount of conspecific pollen transferred.

Plants should allocate resources optimally to nectar defense. If carbon is less limiting relative to other resources for plants growing in the sun, they should allow nectar robbery to occur. Flower species typically found in sunny areas should therefore have fewer defensive morphologies against nectar robbing than flowers found in the shade. We also predicted that this difference in defense should be reflected in a greater occurrence of nectar robbing in the sun because of the increased susceptibility of flowers there.

Methods

On 19 - 20 January 1996 we sampled flower species that occurred almost exclusively in the sun (9 species) or shade (6 species) at the San Luis Cloud Forest Reserve, Guanacaste, Costa Rica. For the first five flowers of each species, we measured defense structures that would make nectar access difficult and pollen contact likely (hole diameter, hole to nectar distance, and pollen to hole distance) . Flower toughness was measured on an index scaled from one (having a corolla but no calyx) to four (having a thickened calyx covering the base of the corolla). Because flowers can employ any or all of these morphological defenses against nectar robbery, we created a total defense index. Each of the four morphological defenses was assigned to an ordinal scale. The indexed values were totaled and scaled 1 - 10, higher numbers being better-defended.

The presence or absence of puncture theft, in which a robber pierces holes in the structures surrounding the nectar, was recorded for 5 - 30 flowers of each species. Percentage of puncture theft in each species was compared between habitats. These data were also analyzed on the community level by comparing total proportion of flowers with puncture theft in the sun and the shade. In patches where insect-flower interactions were occurring as we watched, we recorded incidences of nectar robbery during ten minutes. Because neither the number of puncture thefts nor the individual defense measures met the requirements of normality, data were analyzed using a nonparametric Wilcoxon Rank Sum test. Total defense between habitats was compared using a t-test, and community puncture theft was analyzed with a Chi-square.

Table 1. Measurements of flower morphologies and frequency of nectar robbery of plants in sun and shade habitats at San Luis Reserve.

	Sun (n = 9)	Shade (n = 6)	T [b] or S [c] or X^2	P (mean ± SD)
Hole Diameter [a]	2.67 ± 1.22	2.00 ± 1.26	39.5[c]	0.33
Distance Nectar to Hole (mm)	11.12 ± 12.38	11.43 ± 18.39	42.0[c]	0.52
Distance Pollen to Hole (mm)	3.41 ± 2.29	5.07 ± 7.54	45.0[c]	0.77
Toughness	2.44 ± 1.24	1.33 ± 0.52	34.0[c]	0.09
Total Defense Index	7.06 ± 1.04	5.42 ± 1.35	-2.66[b]	0.02
%Puncture Theft (species)	0.16 ± 0.28	0.07 ± 0.18	35.5[c]	0.19
% Puncture Theft (community)			0.61	0.46

[a] scaled on a 1-4 index

[b] t-test, df = 13

[c] Wilcoxon Rank Sum test

[d] df = 1

Table 2. Measurements of defensive structures for shade and sun flower species.

Species	Hole Diameter (1-4 index)	Pollen to Hole (mm)	Nectar to Hole(mm)	Toughness	Proportion Punctured	Total Defense(1-10 index)
Shade						
Begonia sp.	1	1.00	0	1	0	4.4
?	1	2.78	0	1	0	3.8
?	1	0	1.66	1	0	5.0
?	4	0	1.80	2	0	7.5
?	3	7.23	19.36	1	0	6.3
Razisea sp.	2	19.43	45.77	2	0.44	5.6
Sun						
Buttercup sp.	2	3.20	0	2	NA	6.7
Rubus sp.	1	4.00	1.55	4	0.04	6.3
?	4	1.25	3.00	1	0	6.9
?	1	2.40	4.40	3	0.10	6.3
?	3	5.63	6.07	3	0	6.9
?	4	0.84	6.50	4	0.04	9.4
?	3	6.30	17.25	1	0	6.3
Impatiens sp.	4	0.70	25.57	1	0.26	8.1
Hibiscus sp.	2	6.33	35.75	3	0.82	6.9

NA - data not collected

Results

The four defense morphologies (hole diameter, hole to nectar distance, hole to pollen distance, and toughness) did not differ significantly between sun and shade habitats (Table 1). The combined defense index was significantly greater in the sun than in the shade (Table 1). The proportion of flowers punctured did not differ significantly between sun and shade habitats at either the species level or the community level. In the sun, 11 of the 17 insect visits during 80 minutes of observation were nectar robbery events compared to no visits in 40 minutes of shade flower observation.

Discussion

Contrary to our prediction, the flowers of shade species were not more heavily defended against nectar robbing than sun species. Instead, flower defense actually seemed to be greater in the sun, perhaps as a result of increased visitation by potential robbers in sunny habitats. It was clear from our observations during the study that insects are much more abundant in the sunny habitats than the shady habitats. This may be related to the much higher density of flowers in the sun (pers. obs.), or to the fact that many nectar robbers are poikilotherms who may be less active or abundant in the shade. The costs of nectar robbery are variable— they increase with the amount of robbery which occurs. In contrast, the costs of defense are fixed. Thus, if there is more nectar robbery in the sun than in the shade, there should be selection for plants that direct more resources to nectar defense.

An alternative interpretation is that patterns of floral defense are small and ecologically inconsequential. The magnitude of differences in morphology we observed between habitats was small compared to the tremendous variation in pollination syndrome and defensive structures within habitats (Table 2). This suggests that nectar robbery exerts less influence on floral morphology than pollinator-flower mutualisms. Making nectar less accessible or shifting the location of the anthers may affect which animals can serve as pollinators. Because these defenses would tend to reduce specialization, they might decrease reproductive success through increased pollen dilution or competition. If these reproductive costs are greater than the costs of nectar robbery, then nectar robbery may have little effect on pollinator-flower and interspecific interactions between flowering plants of the cloud forest.

Further research should better quantify differences between nectar robbery in sun and shade, and critically evaluate whether defense costs are significant in terms of whole-plant resource budgets.