EFFECTS OF PATCH SIZE AND BRACT AGE OF HELICONIA WAGNERIANA ON COMMUNITIES OF AQUATIC INVERTEBRATES

Laura C. Broughton, Pamela L. Kunz and Andrew N. Swanson

ABSTRACT (ANS)

Aggregated distributions of Heliconia wagneriana in tropical systems create "islands" for aquatic invertebrates living within bracts. We examined the effects of patch size and bract age of H. wagneriana on the abundance and diversity of invertebrate communities. Based on island biogeography theory and foraging patterns of hummingbird vectors, we predicted that older bracts and larger patches would support a more diverse and abundant invertebrate community. Invertebrate abundance was higher, but diversity was lower in older bracts. Invertebrate abundance per bract was less in large patches of H. wagneriana compared with small patches. Abundance of nematodes was positively correlated with bract density in the patch. Abundance of harpacticoid copepods, and a turbellarian species were positively correlated with total invertebrate abundance. Abundance of syrphids was positively correlated with species richness. Fluid pH within the bracts was substantially more basic than rainwater (7.5-7.9 vs. 6.8), especially in older bracts with less fluid per volume. This research emphasizes three fundamental gaps in our understanding of the invertebrate communities that inhabit Heliconia bracts: the role of pH in shaping community structure; the nature of competitive interactions among invertebrate species; and the mechanisms by which invertebrates disperse among bracts.

Key Words: Heliconia wagneriana , optimal foraging, island biogeography, aquatic invertebrates, hummingbirds.

INTRODUCTION (ANS)

Inflorescenses of the tropical plant Heliconia wagneriana contain volumes of fluid (10-50ml) sufficient to support short-lived communities of aquatic invertebrates. Previous research has focused on the structure of bract communities and factors that determine abundance and diversity (Naeem, 1990). However, the ecology of these communities and the role of external agents remain poorly understood.

Studies of Heliconia have examined the role of resources in bracts (flower parts used by many invertebrates) and their affect on community structure, concluding that the heterogeneous nature of these systems is complex and communities are determined by multiple internal factors (Naeem, 1990). We examined two possible factors external to the bract community that may affect community structure. We hypothesized that variation in the size of H. wagneriana patches, and bract age within patches, may influence the abundance and diversity of invertebrate communities found within bracts.

Because Heliconia inflorescences occur in patches, each patch can be considered a functional "island", isolated from other assemblages. Based upon the equilibrium theory of biogeography, proposed by MacArthur (Begon et al., 1990), communities within these "islands" are affected by patch size, because patch size influences rates of immigration and extinction. In the case of Heliconia, the model predicts that larger patches will experience greater immigration and reduced extinction so that species richness and abundance should increase with island (patch) size. Because some time is required for colonization to occur, and the island community to come to equilibrium, we predict that that

older bracts should harbor more diverse invertebrate communities than younger bracts.

The role of hummingbirds in dispersing invertebrates between H. wagneriana bracts is poorly understood, but it is likely that individuals are transported during hummingbird foraging. Larger patches, because they offer a greater energy return, are visited more often by hummingbirds (Preuss et al., 1993FSP), as predicted by the optimal foraging theory (Begon et al., 1990). If so, invertebrates should be dispersed more frequently between bracts in larger patches. Based upon optimal foraging and island biogeography theory, we predict that the abundance and diversity of species found in H. wagneriana should increase with increasing patch size.

METHODS (LCB)

We sampled four patches of Heliconia wagneriana within a 200m area of La Selva, Heredia Province, Costa Rica, on 14 January, 1994. Two patches were small (17 and 11 inflorescences) and two were large (62 and 57 inflorescences). We sampled two inflorescences per patch and two bracts per inflorescence. Bracts form at the top of an inflorescence; we labeled the bracts starting with the top (and youngest) bract consecutively from number one and took sample from bracts three (5 in Patch 1) and nine. We extracted the fluid within each bract with a 10ml pipet with a 2mm diameter bore and recorded the volume. We then rinsed the bract with 5ml distilled water and extracted the rinse, keeping it separate from the bract fluid. We measured the amount of fluid each bract could contain. Additionally, we measured the area of the patch and recorded the number of bracts and influorescence in each patch.

In the laboratory, using a Corning pH meter 245, we measured the pH of the bract fluids and a vial of rainwater collected during the sampling period. We counted the live invertebrates using stereomicroscopes with no more than 300x magnification. Paramecium and smaller ciliated protozoans were excluded because of their small size.

Diversity was calculated using the Shannon-Wiener Index (Begon, 1990). Patch size, bract age, and size x age interactions were analyzed in relation to bract volumes, pH, abundance, diversity, and species abundances using an ANOVA. All variables were analyzed using a correlation matrix.

RESULTS (PLK)

We collected 320ml of bract fluid, counting 2352 individuals. A total of thirteen species were observed in the bract communities, 9 of which were relatively abundant (Appendix 1). Ephidridae, annelids, Stratiomyidae and Coleopteran larvae were rare and were therefore omitted from the analysis. Actual fluid volume was greater in older bracts ($F_{10} = 17.50$, df = 1, $p < 0.01$) as was possible volume ($F_{10} = 35.16$, df = 1, p = 0.0001). There were significantly more invertebrate individuals in older bracts than in younger bracts ($F_{10} = 6.57$, df = 1, $p < 0.05$) and a trend of decreasing diversity with increasing total abundance. Species richness was significantly greater in smaller

Table 1. ANOVA results (F values) for comparisons of patch size, bract age, patch size x bract age and variation among patches within certain patch sizes compared to other bract variables.

	df	pH	Actual volume	Possible volume	Percent volume	Abundance (# spp.)	Diversity
Patch Size	1	4.15[a]	1.14	0.15	1.07	4.5[a]	0.29
Bract Age	1	6.73[b]	17.50[c]	35.16[e]	2.02	6.57[b]	3.07
Patch Size x Bract Age	1	0.05	3.17	0.99	1.95	1.01	0.19
Variation among patches	2	0.54	3.73[a]	3.04[a]	2.0	2.46	0.10

Error = 10

a: $p < 0.10$ b: $p < 0.05$ c: $p < 0.01$ d: $p < 0.001$ e: $p = 0.0001$

Note: All values except df, pH, possible volume, and percent volume were log transformed log (n + 0.5).

patches than in larger patches ($t = 2.75$, $df = 7$, $p < 0.05$). Nematode abundance varied among patches of the same size ($F_{10} = 9.37$, $df = 2$, $p < 0.01$). Harpacticoids were more abundant in small patches ($F_{10} = 34.26$, $df = 1$, $p < 0.001$) and in older bracts ($F_{10} = 16.34$, $df = 1$, $p < 0.01$).

The effect of bract age was greater in small patches than in large patches for the size x age interaction, ($F_{10} = 13.82$, $df = 1$, $p < 0.01$) Harpacticoid abundance also varied among patches of the same size ($F_{10} = 13.32$, $df = 2$, $p < 0.01$). Syrphidae were more abundant in younger bracts ($F_{10} = 12.81$, $df = 1$, $p < 0.01$) and also varied among patches within a size class ($F_{10} = 4.28$, $df = 2$, $p < 0.05$). Chaoborinae were more abundant in smaller patches ($F_{10} = 10.04$, $df = 1$, $p < 0.01$) and varied among patches ($F_{10} = 5.01$, $df = 1$, $p < 0.05$). The fluid within each bract was significantly more basic in older bracts (pH = 7.94) than younger bracts (pH = 7.49, $F_{10} = 6.73$, $df = 1$, $p < 0.05$). The pH of rainwater was 6.76.

We calculated all possible correlations among the variables in Table 2. The significant positive correlations were: Actual fluid volume vs. possible fluid volume ($r = 0.91$, $p < 0.01$), abundance of nematodes vs. bract density .

Table 2. Means of patch size and bract age categories with significant effects indicated by analyses of variance.

	Patch Size small	Patch Size large	Bract Age young	Bract Age old
pH			7.49	7.94
Actual volume (ml)			14.13	25.88
Possible volume (ml)			16.88	34.00
Abundance*			1.66	2.13
Harpacticoid*	0.85	-0.15	1.05×10^{-3}	0.69
Syrphidae*			0.24	-0.24
Chaoberae*	0.11	-0.30		

*Log transformed abundances log (n+0.5).

($r = 0.69$, $p < 0.01$), abundance of nematodes vs. total abundance of invertebrates ($r = 0.60$, $p < 0.05$), abundance of harpacticoids vs. total abundance of invertebrates ($r = 0.54$, $p < 0.05$), abundance of syrphids vs. diversity ($r = 0.54$, $p < 0.05$), abundance of turbellarian A vs. total abundace of invertebrates ($r = 0.58$, $p < 0.05$). The only negative correlation was pH vs. percent volume of fluid ($r = -0.61$, $p < 0.05$)

DISCUSSION (LCB)

The volume of the bract and the quantity of fluid increased with bract age indicating that the available volume is being filled over time. Presumably, the bract fluid is a combination of Heliconia secretions and rainwater.

When bract fluid levels were low relative to the volume of the bract, the fluid had a higher pH. This suggests that rainwater tends to dilute the fluid and lower the pH. The fluid within younger bracts is not as basic as that in older bracts, suggesting accumulated plant secretions are responsible for the high pH. Alternatively, changes in fluid pH could result from the activity of the invertebrates, but there were no significant correlations between the abundance of any invertebrate group and pH.

The positive correlation between total invertebrate abundance and bract age was consistent with our prediction; older bracts have had more time for invertebrates to colonize their aquatic environments. Additonally, invertebrates like harpactacoids that are late colonizers and/ or exploit resources more common in older bracts have had more time to become established. The decrease in species diversity with increasing bract age (which contradicts our prediction) could be the result of competitive exclusion of some early colonizing species by a few dominant species. Syrphidae seem to be an example of those early colonizers that are weak competitors. The greater species richness with smaller patches may be a result of a dispersal mechanism that favors small patches. Harpactocoid copepods and chaoborinae increased with a decrease in patch size which supports the existence of such a mechanism. The significant variation among ages with a size class for harpactacoids and among patches within a size class for Nematodes, Harpactacoids, Syrphidae, and Chaoborinae indicate the importance of chance in the dispersal of these organisms.

Interpretation of our results requires more understanding of the mechanisms by which organisms disperse from bract to another, and one patch to another. Do hummingbirds transfer them in the course of their visits? Abundance and diversity of invertebrates could ve investigated in relation to number of hummingbird visits per bract per hour. It is also unknown whether the invertebrates that reside in Heliconia bracts have any beneficial or detrimental effects on the plant.

A more complete survey of community composition including more size classes of organisms with better sampling techniques would be beneficial. Our results suggest that pH plays a role in these communities, but we do not know what controls pH or how specific organisms are affected by pH.

Appendix 1. Populations of invertebrates and bract pH over three ages of Heliconia bract

Patch	Bract age	Total Inflorescences	Total bracts	Patch size	Density	Actual vol. (ml)	Possible vol.(ml)	pH	N	HC	T(a)	T (b)	S	C	E	Ch	At	An	St	CL	Sp. X	Total Abundance
1	3	17	102	4.30	23.50	14.50	17.00	7.92	0	0	0	8	9	2	0	3	2	0	0	0	0	24
1	9	17	102	4.30	23.50	37.50	45.00	7.52	0	3	5	262	0	0	0	2	4	0	0	0	0	276
1	3	17	102	4.30	23.50	19.00	24.00	6.94	1	0	9	64	4	0	0	0	8	0	0	0	2	88
1	9	17	102	4.30	23.50	34.00	38.00	7.51	2	10	16	21	1	1	0	8	9	0	0	0	5	73
2	3	11	97	2.40	40.10	10.00	11.00	7.19	35	1	8	21	0	0	0	0	23	0	0	0	0	88
2	9	11	97	2.40	40.10	21.50	29.00	8.03	608	107	4	29	0	2	0	1	24	1	1	0	0	777
2	3	11	97	2.40	40.10	9.00	12.00	7.25	2	14	10	19	1	0	0	0	13	0	0	0	0	59
2	9	11	97	2.40	40.10	26.50	32.00	7.9	19	284	6	5	0	0	0	0	8	0	0	0	0	322
3	3	62	460	31.50	14.60	10.10	13.00	7.69	3	0	0	13	1	0	0	0	25	0	0	0	0	42
3	9	62	460	31.50	14.60	23.00	27.00	8.19	10	0	0	23	0	0	0	0	1	0	0	0	0	34
3	3	62	460	31.50	14.60	18.00	18.00	7.55	2	1	3	5	1	0	0	0	19	0	0	0	0	31
3	9	62	460	31.50	14.60	33.50	44.00	7.67	0	2	1	13	0	1	0	0	0	0	0	0	0	17
4	3	57	414	7.10	58.00	20.50	25.00	7.67	50	0	2	20	2	0	1	0	25	0	0	1	0	101
4	9	57	414	7.10	58.00	11.00	30.00	8.73	169	0	51	3	0	0	1	0	20	0	0	0	0	244
4	3	57	414	7.10	58.00	12.00	15.00	7.66	8	0	1	1	0	2	0	0	0	0	0	0	0	12
4	9	57	414	7.10	58.00	20.00	27.00	7.95	87	0	16	61	0	0	0	0	0	0	0	0	0	164

Key:
N = Nematoda
HC = Harpactacoid copepod
T (a)= Turbellarian (a)
T (b) = Turbellarian (b)
S = Syrphidae
C = Culicinae
E = Ephidridae
Ch = Chaoborinae
At = Anoetidae
An = Annelida
St = Stratiomyidae
CL = Coleopteran larvae
Sp. X : Species X

LITERATURE CITED

Begon, M., J.L. Harper, C.R. Townsend. 1990. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, Boston.

Preuss, C.R., M. B. Royer, M. Seandel. 1993. "Competitive interactions between hermit and non-hermit hummingbirds in relation to patch size of Heliconia pogonantha inflorescences. pages 121-125 in T.S. Bansak and M. Seandel editors, Dartmouth Studies in Tropical Ecology 1993. Dartmouth College: Hanover, NH.

Naeem, S. 1990. "Patterns of the distribution and abundance of competing species when resources are heterogeneous." Ecology, 71: 1422-1429.

Naeem, S. 1990. "Resource heterogeneity and community structure: a case study in Heliconia imbricata [Phytotelmata]." Oecologia, 84: 29-38.