Discussion

Soil heterogeneity: Results supported the prediction that upper horizon soils and soil profiles are more heterogeneous in primary forest than in secondary forest. The greater variation in soil color and organic layer depth in primary forest may indicate greater variation in the amount of aluminum and iron oxides and the organic content in soils. These factors may relate to overall soil nutrient status, which plays an important role in determining plant distribution patterns. Where there is more spatial variation in soil nutrient levels, there is likely to be greater opportunity for a wide range of species to establish. The similarity in variation of soil moisture between primary and secondary forests suggests that water limitation does not have an appreciable effect on ß- diversity.

Gap frequency and size: Gaps occurred in similar frequency between primary and secondary forest, but average gap size was greater in primary forest. Large gaps may create habitats where total incident light levels are ten times higher than in primary forest (Denslow et al. 1987). Bazazz et. al. (1980) found that as gap size increases, branching and advanced regeneration contribute relatively less to gap filling while immigration and seed bank regeneration contribute more. Thus large gaps create opportunities for increased species numbers that are not present in secondary forest where gaps are smaller and more likely to be filled by branching.

Cecropia distribution: *Cecropia* were more clumped in primary forest than in secondary forests, suggesting that with forest maturation Cecropia becomes increasingly limited to rare sites (gaps). Differences in dispersal seem an unlikely alternative explanation given that we observed toucans and other *Cecropia* dispersers in both secondary and primary forest (pers. obs.). Because many of the abundant trees in the secondary forest are pioneer species with life-histories similar to *Cecropia*, it appears that ß- diversity is lower in secondary forest partly because these pioneer species occur in both gaps and in the background forest.

Conclusion: ß- diversity is undoubtedly influenced by a host of factors, including soil heterogeneity, gap size, and life history characteristics of common tree species in the background forest. Even grazing for the relatively short period of 30 years at Corcovado may have been enough to homogenize soils and slow the establishment of edaphic associations in secondary forest. This suggests that the recovery of original patterns of diversity depend not only on the return of primary forest species, but also on the re-establishment of spatial processes that contribute to biotic and abiotic heterogeneity.

Future studies could examine within-forest variation in soil nutrients and correlate them to distribution patterns in the vegetative community. Research could also focus on the relative importance of seed dispersal and pollination in determining tree distribution in primary and secondary forest.

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PROCESSING CHAIN INTERACTIONS BETWEEN DETRIVOROUS INSECT POPULATIONS IN *HELICONIA WAGNERIANA*

Suzanne P. Bird and Christie D. R. Jackson

Abstract. Processing chain models have been used to describe a commensal relationship between midge and mosquito larvae in *Sarraceni purpurea.* The neotropical flower, *Heliconia wagneriana.* appears to harbor a similar community within its bracts, but also includes larvae of the syrphid fly, *Q. Angustriventris* . We hypothesized that syrphids may have either a commensal or an amensal relationship with mosquito larvae. Results suggest that input of dead organic matter is the most important variable in this system, and success is higher for all larvae when resources are abundant. Syrphid abundance was found negatively correlated with mosquito abundance at high resource levels, providing some evidence for an amensal relationship. Patterns of larval success at varying densities and resource levels suggest that the interactions between these three insect larvae are complex and probably not easily explained by a single model.

Introduction

Interspecific interactions are often resource mediated. In addition to competition, these interactions may involve the physical or chemical processing of a resource by one species, that affects its condition for another species (Heard, 1994). In such a "processing chain", resources enter the system in an "upstream" condition and are processed by one consumer to a "downstream" condition, where they are utilized by a second consumer. This chain relationship can be either commensal (+, 0), or amensal (-, 0) (Heard, 1994). The pitcher plant, *Sarraceni purpurea*, contains midge larvae, *Metriocnemus knabi*, which feed on large, coarse dead organic matter (DOM), and mosquito larvae, *Wyeomyi smithii*, which feed on fine particulate DOM. Midges have a positive, commensal relationship with the mosquito larvae because they accelerate the conversion of DOM to small particles, increasing the resource pool available to mosquitoes.

Heliconia wagneriana is a bract flower, similar to the pitcher plant, that is unique to the neotropics and supports a diverse aquatic community containing midge larvae (possibly *Metriocnemus* sp.) and mosquito larvae (*Wyeomyia* sp.), as well as filter feeding, detrivorous syrphid fly larvae (probably *Quichuana angustriventris*). The resource interactions described in the pitcher plant become potentially more complex with the addition of a third player that is likely to be competing for the same DOM input. Two alternate hypotheses were devised for how syrphids fit into the linear processing chain model, and specifically how they might be interacting with the mosquito larvae.

1. *Commensalism*: Syrphids act as an upstream consumer, similar to the midges, and accelerate the conversion of resources to fine DOM. If this hypothesis were supported, we would expect to find some combinations of larval densities or DOM input levels where syrphids are positively affecting mosquito success.

2. *Amensalism*: As an upstream consumer, the syrphids consume either a larger quantity or different quality of resources than the midges, so that they effectively reduce the pool of particulate DOM available to mosquitoes. This type of amensal relationship would be supported if syrphids never had a positive affect, and at times actually had a negative affect, on the survival or success of mosquitoes.

Methods

Our study was conducted on 2-4 January, 1996 at the Sirena Biological Station, Corcovado National Park, Costa Rica. All *H. wagneriana* inflorescences were collected from a large field 50 m from the station on the Sirena trail. Inflorescences were studied in the laboratory within one hour of being picked. We examined 52 bracts. Length and position on the inflorescence were recorded (1 being the bottom, and 12 the top) for each bract. Water was suctioned from the bract and evaluated for DOM using a color index. Six clear vials were filled with bract liquid ranging from clear water (1), to brown liquid (6). This index was used for all measurements of DOM. Bracts were cut open and larvae carefully removed from all flower parts. We counted total numbers of each species, and in a sub-sample we measured the body length (excluding respiratory tube) for at least 5 individuals

of each species present.

To evaluate behavioral interactions between larvae, 15-20 individuals of each species were collected and placed in a large glass jar containing bract liquid. We monitored interactions and feeding behaviors over the next 24 hours, watching closely for signs of aggression or interference competition. Relative feeding rates of all larval species were experimentally measured by placing three larvae of one species in a vial containing 25 ml of bract liquid (DOM = 6), and re-evaluating the DOM content after 24 hours. Three replicates were done for each species.

Results

In 24 hours, syrphids reduced the DOM index from 6 to 1, while midges and mosquitoes only reduced the DOM index from 6 to 4. Although this difference could result from the syrphid's larger biomass, their effect on DOM availability to mosquitoes still is pronounced. We saw no interspecific aggression when species were combined, however larval stratification was apparent: midges remained in settled DOM, mosquitoes remained suspended near the top, and syrphids were prevalent throughout. Syrphids tended to be the most motile, moving throughout the column.

Lower bracts (position 1-4 on the inflorescence) were larger and contained more concentrated DOM (Table 1). Increased DOM was correlated with larger midges, mosquitoes, and syrphids, but were also correlated with reduced mosquito numbers (Table 1 and 2, Figure 1). Syrphid length was correlated with lower mosquito numbers but greater mosquito length in both high and low bracts (Figure 2 and 3).

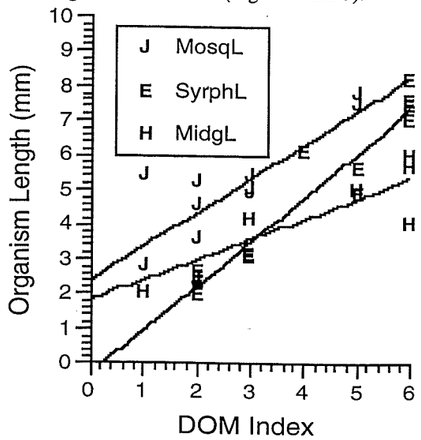

Fig. 1. Correlation of mosquito, syphid, and midge length with increased DOM.

Discussion

In their contained community, syrphid and mosquito success may depend on DOM resource availability, intraspecific competition, and interspecific interactions. These variables were examined based on syrphid and mosquito success. Larval length, rather than number is a better success indicator due to laid egg variance (5 - 40) between bracts.

In this study, we concluded that DOM plays an essential role in the syrphid / mosquito relationship that previously had been ignored. High DOM was correlated with increased larval size and presumably increased per capita reproductive rates. Because commensal or ammensal relationships would be expected to change with DOM input, we analyzed high and low position bracts (representing low and high DOM) separately to reveal interactions that may not otherwise appear. Previous studies (Broughton et. al, 1994) suggested organism size was a function of bract age, citing older bracts allow longer larvae maturation. Syrphids mature in 55 days, yet successive heliconia bracts opens every 2 days (Janzen, 1983). Two days of syrphid growth would not account for the size differences seen between bracts.

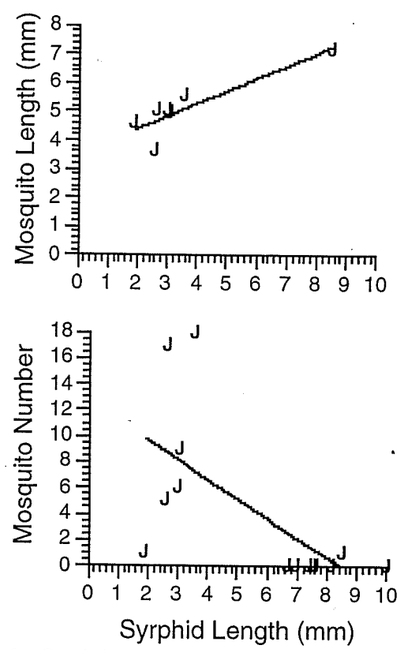

Fig 2: Correlation of syrphid length with both mosquito number and mosquito length in low bracts (with high DOM).

Table 1: Mean lengths and numbers of mosquitoes, midges, and syrphids at different DOM levels

DOM index	Mosquito length (mm)	Syrphid length (mm)	Midge length (mm)	# of Mosquitoes	# of Syrphids	# of Midges
2	3.5 + 0.6	2.3 + 0.2	--	7.3 + 4.3	4.8 + 1.7	0.0 + 0.0
3	5.1 + 0.1	3.1 + 0.0	4.2 [a]	7.7 + 0.8	16.7 + 12	0.3 + 0.3
4,5	7.6 + 0.1	5.5 + 0.3	5.0 [a]	0.8 + 0.5	6.3 + 1.4	0.3 + 0.3
6	--	7.5 + 0.2	5.2 + 0.6	0.0 + 0.0	8.5 + 1.9	2.0 + 1.4

[a] n = 1

Table 2: Correlation matrix of bract characteristics (n = 51 bracts for bract position, bract length, midge number, syrphid number, and mosquito number; n = 33 bracts for DOM, mosquito length, syrphid length, and midge length).

	Bract Pos	Bract L	DOM	Midge #	Mosq #	Syrph #	Mosq L	Syrph L
Bract Pos	--	--	--	--	--	--	--	--
Bract L	-0.85***	--	--	--	--	--	--	--
DOM	-0.54*	0.17	--	--	--	--	--	--
Midge #	-0.23	.023	0.41	--	--	--	--	--
Mosq.#	-0.11	0.33*	-0.66**	-0.19	--	--	--	--
Syrph #	-0.45	0.39**	0.19	0.27	0.00	--	--	--
Mosq L	-0.08	-0.03	0.80**	0.02	-0.13	0.12	--	--
Syrph L	-0.14	-0.05	0.96***	0.25	-0.58*	-0.17	0.75**	--
Midge L	-0.43	0.05	0.85*	0.14	-0.60	0.22	0.94	0.46

*$p < 0.025$; **$p < 0.005$; ***$p < 0.0001$

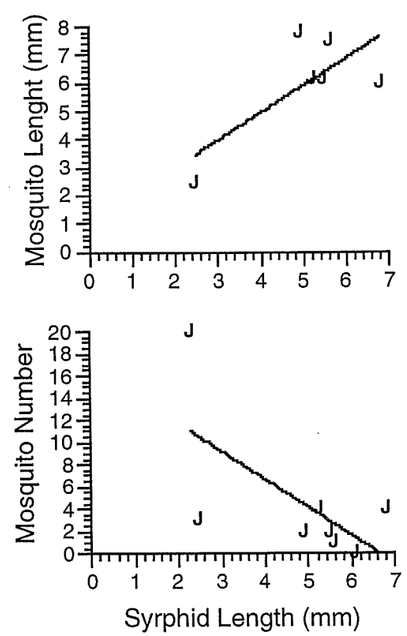

Fig 3: Correlation of syrphid length with both mosquito number and mosquito length in high bracts (with low DOM)

Differences in larvae success seemed to result mainly from interspecific interactions and not from intraspecific competition. Theoretically, intraspecific competition occurs when larval abundances are high, decreasing resource availability per individual. Thus, when larval numbers increase, larval size is expected to decrease. However, there were no significant correlations (negative or positive) for any of the species suggesting that intraspecific competition may be minimal.

At high DOM levels (low bracts), interspecific interactions showed both ammensal and commensal characteristics. Syrphid and mosquito lengths increased together, while mosquito numbers decreased. At the population level, ammensalism may out-compete mosquitoes for resources, causing decreased mosquito survival and growth. However, at the individual level, commensalism may occur because the surviving mosquitoes would have more resource per individual. This could lead to an increase in the mean fecundity of those individuals that survive to become adults. Thus, interspecific interactions between syrphids and mosquitoes may indirectly be influencing mosquito intraspecific competition.

At low DOM levels (high bracts), there was no evidence of ammensalism. Instead, there was a positive

correlation between syrphid length and mosquito length. If ammensalism were evident, one would expect to see syrphids dominating and mosquitoes losing out on the limited DOM resources. If ammensalism occurred, it should be intensified at low DOM levels due to increased competition.

This study leaves an essential question unanswered: what causes the positive correlation between syrphid and mosquito size? It may be due to (1) commensalism in the processing chain, or (2) a surplus of DOM relative to the needs of the mosquitoes so that competition which would not be visible with a DOM overabundance. By experimentally manipulating syrphid numbers, the true nature of this correlation would appear. If competition was prevalent, mosquito size would decrease, while commensalism would increase mosquito size.

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