WEAK COMPETITION BETWEEN COASTAL INSECT HERBIVORES

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Abstract

Related communities of four to seven insect herbivore species commonly feed on each of the coastal plant species *Borrichia frutescens* (L.), *Iva frutescens* (L.), and *I. imbricata* Walt. which grow on spoil islands in west-central Florida. Most stems of these host plant species show no evidence of herbivory or of actively feeding herbivores. At the scale of within *Iva* bushes or *Borrichia* patches on islands, there were significantly fewer co-occurrences of herbivores on individual stems or terminals than expected, suggesting competition is important on a small scale in this system. However, at the scale of between patches of host plants, that is, between islands, there were no negative correlations between herbivores which suggests that competition is unimportant in influencing the distribution of these species at larger spatial scales. At large spatial scales, other phenomena such as host plant genotype or environmental (island) variability may be more important in influencing the distribution of herbivores.

Key Words: competition, co-occurrences, coastal plants, *Borrichia frutescens*, *Iva frutescens*, *Iva imbricata*, insect herbivores, Florida

RESUMEN

Comunidades de cuatro a siete especies de insectos herbívoros comúnmente se alimentan de las plantas costeras *Borrichia frutescens* (L.), *Iva frutescens* (L.) e *I. imbricata* Walt., las cuales crecen en islas ubicadas al oeste del centro de la Florida. La mayoría de los tallos de estas plantas huéspedes no muestran evidencia de actividad por parte de herbívoros. En plantas de *Iva* o en manchones de plantas de *Borrichia* se encontraron significativamente menos co-ocurrencias de herbívoros en tallos individuales o ramas terminales de lo esperado. Esto sugiere que la competencia es importante en pequeña escala dentro de este sistema. Sin embargo, a nivel de manchones de plantas huéspedes, es decir, entre islas, no se encontraron correlaciones negativas entre herbívoros, lo cual sugiere que en una escala espacial mayor, la competencia no influye de manera importante en la distribución de estas especies. Al nivel de escalas espaciales mayores, otros factores como el genotipo de la planta huésped o la variabilidad ambiental (isla) podrían influír de manera más importante sobre la distribución de herbívoros.

INTRODUCTION

The role of interspecific competition in ecological theory has changed through the years. Many studies in the 1970's viewed a lack of co-occurrences between possible competitors as a possible indicator of competition, reasoning that interspecific competition can cause negative associations (Strong 1982, Strong et al. 1984). In the early 1980s, phytophagous insects were seen as infrequent competitors possibly because their small size makes them especially vulnerable to predators which reduce population sizes to levels below which competition is important (Connell 1983). In the mid 1980s a series of experimental studies found that competition among herbivorous insects may be much more important than previously believed (Stiling and Strong 1984, Fritz et al, 1986, Faeth 1987, Crawley and Pattrasudhi 1988, Mopper et al. 1990, Moran and Whitham 1990, Damman 1993). By the mid 1990s enough evidence had accumulated to suggest that competition between phytophagous insects was probably as common as in other taxa, occurring in 76% of case studies (Denno et al. 1995). In spite of the increased recognition of interspecific competition, there remains relatively little progress in demonstrating where or when competition is likely to be important in insect communities (Denno et al. 1995). Is competition a strong enough phenomenon across all spatial scales to shape community structure and patterns of co-occurrence or is it only important at small scales and so weak that it cannot structure communities across broader geographic regions? Ricklefs and Schluter (1993) suggested that different ecological processes act on different scales and that interactions between species, such as competition and predation, would occur at relatively small scales. In support of this, extensive studies on the diversity of insects feeding on bracken revealed that competition was weak and occurred only at small scales (Lawton et al. 1993). Our study focuses on co-occurrences between insect herbivores attacking three species of coastal plants in west-central Florida: *Borrichia frutescens* (L.) de Candolle, *Iva frutescens* L. and *Iva imbricata* Walt. Here, lack of co-occurrence is taken as a possible indication of interspecific competition. We first examine the extent of co-occurrences on a small scale, between bushes or patches of individual host plants, and then examine competition at a larger scale, between islands.

METHODS

The study system

A natural intracoastal waterway runs between the mainland and the barrier islands of many coastal states. To facilitate boat traffic, the U.S. Army Corps of Engineers often deepen these natural channels by dredging. Along the Florida coast, this dredge material was typically heaped together as small "spoil islands" that were placed adjacent to the main channel at regular intervals of about 0.5 kilometers. Such islands off the Pinellas County coast served as our study sites.

Most islands support some vegetation. Typically, they are overgrown by the invasive exotics Brazilian pepper and Australian pine in their centers, but a few palms may be present as well. Red, black and white mangrove, along with small patches of salt marsh cordgrass grow near the waterline. Between the waterline and the island centers, three other native plants can be relatively common: sea daisy, *Borrichia frutescens*, marsh elder, *Iva frutescens* and beach (or dune) elder, *Iva imbricata*. The phytophagous insect community on these hosts does not occur on any other plant species on these islands.

Islands usually have either one or two (rarely all three) of these host species. The three host plants do not commonly intermingle. *Borrichia* grows as clonal patches on saturated silty sands. *Iva frutescens* requires slightly higher elevations and prefers lower-salinity soils, often in stonier ground. *Iva imbricata* is most common on beaches or sand dunes and prefers islands with sandier soils (Barnett and Crewz 1990). Islands may or may not have all of these habitat types present, but if they do, these species tend to grow adjacent to one another, not interdispersed. Sometimes the *Iva* species may shade *Borrichia*, but only at the edge of the patch. The patchy nature of plant distribution between these islands mimics what occurs in mainland areas where patches of *Borrichia* and *Iva* are separated by salt pans, needle rush, saltmarsh cord grass or other vegetation (Stiling and Rossi 1994).

Insect herbivores

Borrichia frutescens, *I. frutescens* and *I. imbricata* have many genera of their insect herbivores in common (Table 1). The gall maker, *Asphondylia borrichiae* Rossi and Strong, exists as two races, one of which attacks *Borrichia* almost exclusively, and one, which we call *A.* sp nr *borrichiae*, which attacks *Iva* sp. (Rossi et. al. 1999) but which prefers *I. frutescens* (see also Rossi and Stiling 1995). Two species of *Pissonotus* planthoppers, *P. quadripustulatus* (Van Duzee) and *P. albovenosus* Osborn, suck the sap of leaves and stems. *Pissonotus quadripustulatus* feeds only on *B. frutescens*, while *P. albovenosus* feeds exclusively on the two *Iva* spp. with *Iva imbricata* the preferred host (Stiling and Rossi 1995). Another sap sucker, the aphid *Dactynotus* sp., feeds on *Iva* sp. but is most commonly found on *I. frutescens* (Ferguson and Stiling 1996). A related species which we call *Dactynotus* sp. green feeds on *Borrichia*. The third common sap sucker is a spittlebug, *Philaenus* sp., individuals of which are protected inside spittle masses. These are much more numerous on *I. imbricata* than on the other host species, *I. frutescens*. Cecidomyiid stem borers are common on both species of *Iva* but are not present on *Borrichia*. We noted a lepidopteran stem borer in *Borrichia*, but it was much less common and we were unable to rear adults of this species. *Buccalatrix* leafminers leave characteristic thin, serpentine, mines on host leaves and are only present on *I. frutescens*. A seventh herbivore, an eriophydid mite, creates numerous leaf galls on *I. frutescens*, with up to 100 galls on a single leaf. Each gall contained up to 50 mites and some bushes are heavily infested. This was the most common herbivore on *I. frutescens*, but it was never found on the other two host plants.

There are two other broad categories of herbivores. The first is "other sap-sucking homopterans" which included *Carneocephala floridana* Ball, which is known to use *Borrichia* extensively in north Florida (Rossi and Strong 1991), the exotic cottony cushion scale, *Icerya purchasi* Maskell, and other scale insects. These other sap suckers are never common on most of the study islands. The other guild is the leaf chewers, and this group includes various grasshoppers, crickets, beetles, caterpillars and the stick insect, *Anisomorpa buprestiodes* (Stoll), but again these insects are rare and, on average, never infest more than 0.3% of the stems on any host plant species.

Censuses

On eight islands with *Borrichia*, eight with *I. imbricata* and 15 with *I. frutescens*, we counted the number of each species of insect occupying each stem on three sets of 30 stems, or ramets, in three areas of a *Borrichia* patch or three sets of 30 branches or terminals on each of three *I. frutescens* or *I. imbricata* bushes. Most insects were easily visible to the naked eye except stem borers, gall makers and spittle bugs. Density estimates of stem borers were assessed by counting exit holes on stems. Densities of gall makers and spittle bugs were assessed by counts of galls and spittle masses, respectively. Censuses were performed bi-monthly starting in February and ending in October in both 1992 and 1993 so as to encompass two years and multiple generations of insects. One partial data set, for *Borrichia* in February 1992 was lost. Presumed competition at the level of within islands on a patch of *Borrichia* or bush of *Iva* was assessed by comparisons of the presence, absence and co-occurrence of each species of herbivore on all stems combined for each plant species (Rathcke 1976). Statistical analyses were performed using X^2 tests, but species combinations were tested only where there was sufficient power to detect significant differences if they were present (Bultman and Faeth 1985). Competition at the level of between islands was assessed by correlating total abundance of each herbivore species, February 1992-October 1993, between islands.

RESULTS

There are at least four common herbivores on the *Borrichia*/*I. frutescens*/*I. imbricata* community: the gall making fly *Asphondylia*, the sap sucking planthoppers *Pissonotus* spp., the sap sucking aphids, *Dactynotus* spp., and the stem boring fly *Neolasioptera* (Table 1). In addition, an eriophydid mite is common on *I. frutescens*, a sap sucking cercopid, *Philaenus* is present on *I. imbricata* and a leaf miner, *Buccalatrix*, occurs on *I. frutescens*. However, most stems on any one host plant exhibit no herbivores or signs of herbivory. The percentage of empty stems is, on average, 85.1% for *Borrichia*, 79.9% for *I. imbricata* and 65.1% for *I. frutescens*.

At the scale of a *Borrichia* patch or *Iva* bush, there were many fewer co-occurrences of herbivores together on individual stems than expected (Tables 2-4). On *Borrichia* the co- occurrence of the gall maker *Asphondylia* and the sap sucking *Pissonotus* was not significantly different than expected, but the co-occurrences of the two sap suckers, *Pissonotus* and *Dactynotus* were low, and approached statistical sig-

TABLE 1. HERBIVORES OF *BORRICHIA FRUTESCENS*, *IVA FRUTESCENS* AND *IVA IMBRICATA*, BASED ON SAMPLES OF 7200 RAMETS PER ISLAND DURING 1992 AND 1993.

Herbivore	Type of herbivore	Percent of stems infested		
		B. frutescens	*I. frutescens*	*I. imbricata*
Asphondylia borrichiae	stem galler	3.3	0	0
Asphondylia sp nr *borrichiae*		0	6.3	2.1
Pissonotus quadripustulatus	planthopper	9.3	0	0
Pissonotus albovenosus		0	3.8	9.3
Dactynotus sp brown	aphid	0	4.9	1.3
sp green		1.8	0	0
Neolasioptera	stem borer	0	3.6	5.5
Buccalatrix sp	leaf miner	0	1.2	0
Phinaenus	spittlebug	0	0.1	1.1
eriophydid mite	leaf galler	0	20.7	0
other homopterans	sap suckers	0.1	0.4	0.3
various spp	leaf chewers	0.2	0.3	0.2

nificance (P = 0.06). For *Iva imbricata*, *P. albovenosus* and *Dactynotus* co-occurred less frequently than expected, but the sap sucking spittle bug, *Philaenus*, did not occur less frequently with *P. albovenosus* than expected. The stem borer *Neolasioptera* co-occurred relatively infrequently with galls of *Asphondylia* sp. nr *borrichiae* (P = 0.082) and this result was not entirely unexpected as stem boring often kills the apical meristem above the bored portion of the stem. Thus, the presence of *Neolasioptera* may

TABLE 2. CO-OCCURRENCES OF HERBIVORES ON 6900 *BORRICHIA FRUTESCENS*.

Herbivore Species			X^2	P
	Pissonotus quadripustulatus			
Asphondylia borrichiae	Present	Absent		
Present	16	209	1.10	0.294
Absent	628	6047		
	Dactynotus sp			
Pissonotus quadripustulatus	Present	Absent		
Present	5	639	3.58	0.06
Absent	119	6137		

TABLE 3. CO-OCCURRENCE OF HERBIVORES ON 7200 *IVA IMBRICATA* STEMS.

Herbivore species			X^2	P
	Pissonotus albovenosus			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	3	150	9.194	0.002
Absent	670	6377		
	Neolasioptera			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	5	148	3.024	0.082
Absent	394	6655		
	Neolasioptera			
Pissonotus albovenosus	Present	Absent		
Present	3	670	35.76	<0.001
Absent	396	6131		
	Dactynotus sp			
Pissonotus albovenosus	Present	Absent		
Present	2	671	5.124	0.024
Absent	93	6434		
	Philaenus sp			
Pissonotus albovenosus	Present	Absent		
Present	11	662	1.851	0.174
Absent	69	6458		

prevent *Asphondylia* galls from developing, because they occur only on the apical meristems. Few co-occurrences were also noticed between *Neolasioptera* and *P. albovenosus* and between *Asphondylia* and *P. albovenosus*. For *Iva frutescens*, co-occurrences were significantly less than expected for every combination of insect herbivores tested, except those involving the eriophydid mite, and even here there was a significant lack of co-occurrences with the sap sucker *P. albovenosus* and a marginally significant lack ($P = 0.065$) with the sap sucker *Dactynotus* sp brown. At the larger scale of between islands there were no significant negative correlations between species abundances (Table 5). Similar results were observed when the correlations used total insect abundance instead of proportion of stems infected.

DISCUSSION

There are several conclusions from the present study. The first is that the occupancy of stems of *Borrichia frutescens*, *Iva frutescens*, and *Iva imbricata* is low, with the majority of stems having no herbivores. Interestingly, Root and Cappuccino (1992) also found low herbivore loads on goldenrod (*Solidago*) in New York, where the entire fauna weighed <1% of the leaf mass. Why stem occupancy rates are so low in our system remains a mystery. It was, therefore, a surprise that we found so few co-occurrences at the scale of a *Borrichia* patch and at the scale of individual bushes for *I.*

TABLE 4. CO-OCCURRENCE OF HERBIVORES ON 13500 *I. FRUTESCENS* STEMS.

Herbivore species			X^2	P
	Pissonotus albovenosus			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	3	847	26.92	<0.001
Absent	488	12162		
	Neolasioptera sp			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	10	840	16.07	<0.001
Absent	499	12151		
	Dactynotus sp			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	22	828	10.08	0.001
Absent	644	12016		
	Eriophydid mite			
Asphondylia sp nr *borrichiae*	Present	Absent		
Present	163	687	1.299	0.254
Absent	2641	10009		
	Neolasioptera sp			
Pissonotus albovenosus	Present	Absent		
Present	3	488	13.13	<0.001
Absent	506	12503		
	Dactynotus sp			
Pissonotus albovenosus	Present	Absent		
Present	6	485	14.15	<0.001
Absent	660	12349		
	Eriophydid mite			
Pissonotus albovenosus	Present	Absent		
Present	37	454	53.40	<0.001
Absent	2767	10242		
	Dactynotus sp			
Neolasioptera sp	Present	Absent		
Present	6	503	15.08	<0.001
Absent	660	12331		
	Eriophydid mite			
Neolasioptera sp	Present	Absent		
Present	120	389	2.355	0.125
Absent	2684	10307		
	Eriophydid mite			
Dactynotus sp	Present	Absent		
Present	119	547	3.403	0.065
Absent	2685	10149		

TABLE 5. PEARSON CORRELATIONS OF HERBIVORE DENSITIES (PROPORTION OF INFESTED STEMS) BETWEEN NATURAL PATCHES OF *B. FRUTESCENS* (N = 8), *I. FRUTESCENS* (N = 15) AND *I. IMBRICATA* (N = 8) DURING 1992/93 * = SIGNIFICANT AT P < 0.05.

Plant species		Herbivore species				
B. frutescens		*A. borrichiae*	*P. quadripustulatus*			
	P. quadripustulatus	-0.371				
	Dactynotus sp	-0.129	-0.329			
I. frutescens		*A.* sp. nr. *borrichiae*	*P. albovenosus*	*Dactynotus* sp	*Buccalatrix* sp	*Neolasioptera* sp
	P. albovenosus	-0.282				
	Dactynotus sp	-0.209	-0.395			
	Buccalatrix sp	0.377	-0.131	-0.325		
	Neolasioptera	-0.262	-0.507	-0.310	0.451	
	Eriophydid	0.236	-0.289	0.140	0.303	0.438
I. imbricata		*A.* sp. nr. *borrichiae*	*P. albovenosus*	*Dactynotus* sp	*Neolasioptera* sp	
	P. albovenosus	-0.386				
	Dactynotus sp	-0.389	-0.339			
	Neolasioptera sp	-0.311	-0.182	0.216		
	Philaenus sp	-0.215	0.486	0.042	0.101	

frutescens and *I. imbricata*. Taking all host plant species together, co- occurrences were significantly lower (P < 0.05) in ten pairwise comparisons, marginally significantly lower (0.05 > P < 0.10) in three cases and non-significant (P > 0.10) in four cases. However, even in the non-significant cases the trend was towards fewer co-occurrences than expected. It is instructive to realize that while a lack of co-occurrences could indicate competition in this system, lack of interspecific association could also be caused by other factors such as differential attractiveness to certain stems by certain herbivore species. These methodological problems probably helped push competition studies towards experimental manipulations in the 1980s and beyond. However, the lack of co-occurrences is at least consistent with the idea that competition may be occurring at the spatial scale of between bushes or patches. Some of the competitive interactions at this scale may actually be amensalism (Lawton and Hassell 1981). For example, stem borers and gall makers do not commonly co-occur probably because the stem borer makes the stem unsuitable for the gall maker, not vice-versa. However, without detailed experimental studies of the effect of each species on the other, the exact ratio of amensalism to competition in this community remains difficult to assess.

Although presumed competition appeared frequently on a small scale in this community, as evidenced by virtue of the lack of species co-occurrences, it does not appear strong enough to shape distribution patterns of herbivores between islands. There were no significant negative correlations between herbivores between *Borrichia* patches or *Iva* bushes between islands. Our previous reciprocal transplant experiments, involving plants of different genotype between islands, have shown that host plant genotype and environmental variation both play major roles in shaping the distribution patterns of insects between islands (Stiling and Rossi 1995, 1996). Environmental and genetic variation between islands is probably so great that it swamps any effect of competition on the distribution of insect herbivores. Only when both genotype and environmental variation are minimized, as on small individual bushes, can the relatively small effects of competition be seen. Thus, in general, our results support the ideas of Ricklefs and Schluter (1993) that ecological phenomenon may operate only at certain scales and that the effects of competition operate primarily at small spatial scales.

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