

## ECOTOPE DIFFERENTIATION IN A GUILD OF SAP-FEEDING INSECTS ON THE SALT MARSH GRASS, *SPARTINA PATENS*<sup>1</sup>

ROBERT F. DENNO

Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

**Abstract.** Niche and habitat differentiation are studied in seven sap-feeding insects (mostly leafhoppers and planthoppers) that inhabit the salt marsh grass *Spartina patens*. The microhabitat niche dimension is well partitioned. Four species of sap-feeders occur primarily in the upper stratum of the grass system, while three others are abundant in and beneath the lower thatch layer. Conversely, the seasonal niche dimension is poorly partitioned and most species show similar phenologies. The elevational habitat dimension is also poorly partitioned where most of the sap-feeders occur most abundantly on patches of grass within 10 cm of mean high water level. There are sufficient differences in resource utilization along niche and habitat dimensions as well as body size to explain the coexistence of all sap-feeders but two. The niches and body sizes of *Amplicephalus simplex* and *Aphelonema simplex* are very similar. One of these species, the leafhopper, *Am. simplex*, is the only species that fully retains the ability to fly. Populations of the other seven species are composed mostly of flightless brachypterous wing-morphs. It is hypothesized that *Am. simplex* is able to coexist in the guild because it is able to efficiently colonize relatively empty (competitor-free) patches of grass created by the catastrophic effects of storm tides.

**Key words:** ecotope; elevational distribution; leafhopper; microhabitat distribution; niche; plant-hopper; resource partitioning; salt marsh; sap-feeding insects; seasonal distribution; *Spartina patens*.

### INTRODUCTION

The vegetation of East Coast North American intertidal marshes from Nova Scotia south to northern Florida is dominated by several species of grasses and rushes (Teal 1962, Adams 1963, Blum 1968, Redfield 1972, Duncan 1974, and Hatcher and Mann 1975). Although these plants are fed upon by a number of functional feeding groups of insects (e.g., stem borers and strip-feeders), the most abundant herbivorous insects are sap-feeders in the suborder Auchenorrhyncha (leafhoppers and planthoppers) (Teal 1962, Davis and Gray 1966, Denno 1976, 1977, 1978, Webb 1976, and Denno and Grissell 1979). The number of resident species of sap-feeders associated with each plant species differs. For instance, in the Mid-Atlantic states, nine sap-feeders occur on *Spartina patens* (Salt Meadow Hay), eight on *Distichis spicata* (Salt Grass), four on *Spartina alterniflora* (Salt Marsh Cord Grass), while only two species exploit *Juncus roemerianus* (Needle Rush) (Denno 1976, 1977, 1978). The large number of abundant, host specific, sap-feeding species associated with *S. patens* provides an excellent opportunity to explore some of the mechanisms that allow for species coexistence.

Hutchinson (1953) suggests two situations in which competing species may coexist without achieving a stable equilibrium. First, non-equilibrium coexistence can be attained by organisms with several generations per year where changing environmental conditions can shift species dominance, preventing any one species from excluding the other. Secondly, a non-equilibrium

community is possible if catastrophic events continually destroy existing habitats while creating new ones. Under these circumstances, competitively weaker species may coexist because of their increased ability to disperse and colonize vacant sites.

McClure and Price (1975) suggest that coexistence in a guild of sycamore-feeding leafhoppers may be partially explained by frequency-dependent competitive ability since at high densities each species adversely affects its own fitness more than that of its competitors. Lastly, coexistence in equilibrium communities may be achieved by resource partitioning, whereby species may reduce interspecific competition by exploiting different aspects of the same resource (Schoener 1974). Andrzejewska (1965), McClure (1974), and Halkka et al. (1977) found that each species of sap-feeder, whether associated with meadow communities or sycamore trees, tended to occur at a particular level in the vegetation or on different parts of the leaf. McClure (1974) suggests that the sycamore leaf offers a mosaic of microhabitats which allows for niche diversification and specialization among the guild members.

Ultimately, my goal is to determine the mechanisms which allow for the coexistence of the sap-feeding species of insects associated with *S. patens*. Questions that eventually must be addressed in detail concern the equilibrium state of the community, the degree to which resources are limiting, the relative competitive and dispersal abilities of the sap-feeders, and differences in the way each species uses the resource. In this report, I concentrate on the last of these questions and study resource partitioning in the guild of sap-feeders by using one habitat factor (marsh elevation)

<sup>1</sup> Manuscript received 14 December 1978; accepted 11 May 1979; final version received 25 July 1979.

and two niche factors (microhabitat distribution within the grass system and temporal utilization) (see Whitaker et al. 1973 and McClure and Price 1976 for a discussion of habitat, niche, and ecotope factors). Lastly, I rank the importance of the three ecotope dimensions according to the degree that each is partitioned by the sap-feeding insects.

#### DISTRIBUTION, STRUCTURE AND GROWTH DYNAMICS OF *SPARTINA PATENS*

*Spartina patens* is one of the dominant components of salt marshes and sandy beaches along most of the Atlantic and Gulf Coasts of North America (Mobberley 1956). The grass occupies a narrow elevational zone of well-drained soil above mean high water level (MHW) where it can grow in extensive pure stands that are occasionally inundated by tides (Blum 1968, Redfield 1972). Extensive pure stands (>1 ha) are common along the Atlantic Coast from Virginia north. South of Virginia on the Atlantic and along the Gulf Coast, *S. patens* usually occurs as a narrow broken fringe of vegetation along the high marsh and is commonly mixed in with other halophytic plants (Mobberley 1956, Blum 1968, and Redfield 1972). Here, the large expanses found along the coasts of the Mid-Atlantic and New England states are rare.

*Spartina patens* is a slender-culmed grass with narrow, convoluted blades (Mobberley 1956, Blum 1968). The culms grow and project through a thick (5–20 cm), dead, horizon of prostrate culms and blades resulting from the previous years' growth. New culms, shaped like vertical awls, first protrude through the thatch in spring. As the season progresses, older leaf-blades separate from newer, upright ones by bending at the sheath-blade junction. As subsequent blades fold back in this fashion, they make contact with the surface of the dead thatch. By summer, the dead thatch becomes overlaid with an entanglement of living leaf-blades. Further prostration occurs in summer and fall, when the culms fold over at a weak area in the stem which coincides approximately with that portion of the stem that is included in and surrounded by the dead thatch (Blum 1968). Prostration usually occurs in a mosaic fashion, leaving behind "islands" of somewhat erect plants. On Mid-Atlantic and New England marshes, flowering occurs from June through September.

If the structure of *S. patens* is examined during summer, one finds an uppermost layer of living, partially prostrate grass overlying a dead horizon of dry culms from the previous year. Beneath this dry horizon is a layer of entangled moist culms and blades 2 and 3 yr old. Between the moist layer of culms and the marsh surface is a horizon of decaying grass older than 3 yr. Often, near the base of individual plants, the lower layer of thatch fails to contact the surface of the marsh because it is suspended by the dense crowns of the individual plants. Young tillers commonly protrude from the crown into the open space. Also, foraging

voles (*Microtus*) create a labyrinth of tunnels underneath the thatch and appear to play an important role in maintaining this open space at certain locations.

#### STUDY SITE AND METHODS

##### *Study site*

The primary study site was an Atlantic coastal marsh in the Mullica River-Great Bay estuarine system where Great Bay Boulevard crosses over Little Thorofare Creek, Tuckerton, Ocean County, New Jersey, USA. The marsh vegetation was dominated by the two marsh grasses *Spartina patens* and *S. alterniflora* growing in a mosaic-like pattern of pure patches. All insect samples at the Tuckerton study site were taken in patches of *S. patens* that ranged in size from 500 to 1000 m<sup>2</sup>.

##### *Microhabitat distribution of sap-feeders*

The *S. patens* grass system was divided into five rather distinct vertical zones (see the definition of zones in the stylized representation of the grass system at the top of Fig. 2). Zone five consisted of the seed heads and terminal blades of the upright living grass. Zone four comprised subterminal blades and stems of the living grass and was like zone five except that most plant parts were shaded. Prostrate living culms and blades knocked over by winds formed zone three. A thatch layer of horizontal dead culms and blades through which passed the basal portion of ensheathed, vertical, living culms defined zone two. Zone one consisted of the crowns and tillers of the grass beneath the thatch layer.

The distribution of each sap-feeder among the profile of five zones was determined by carefully sorting through a 0.3-m<sup>2</sup> swath of each stratum by hand and scoring the number of each species. Separate but nearby swaths of vegetation were used for each stratum. The profile of five samples was replicated 13 times during June–August 1976.

##### *Elevational distribution of sap-feeders*

The relative elevations of eight similar-sized patches of *S. patens* were determined by using a transit. Patch elevations ranged from ≈MHW to nearly 25 cm above, representing the entire elevational range of *S. patens* on the Tuckerton marsh. By using a standard sweep net, sap-feeders were sampled in eight patches of grass along the elevational gradient. A sweep sample consisted of 10 random sweeps to and fro with the net taken while walking through the vegetation. Five sweep samples were taken in each patch during May, July and August. To insure that sap-feeders inhabiting the lower strata were collected, an insect vacuum (D-vac) was also used. Each sample consisted of four applications of the vacuum sampler (each at a compass point) to the grass surface at a randomly chosen location in the vegetation. D-vac samples (five per

patch) were taken only during August. Samples were returned to the laboratory where insects were sorted to species and counted.

#### Seasonal distribution of sap-feeders

Seasonal distributions for sap-feeders inhabiting *S. patens* on New Jersey salt marshes were determined by data (mean density per month) from Denno (1977) and Raupp and Denno (1979). Thus, seasonal distributions were based on 12 points.

#### Body mass relationships

The average dry mass of each sap-feeder species was determined by weighing five groups of 10 insects each (5♂'s and 5♀'s).

#### Analyses

The degree to which the various sap-feeders specialized in their exploitation of resources (=relative niche width) along the three ecotope dimensions was determined by using the following formula (Levins 1968):

$$B = 1 / \sum_{i=1}^n p_i^2 / n$$

where  $B$  is relative niche width,  $P_i$  is the proportion of a species (expressed as a decimal) in the  $i^{\text{th}}$  unit of the resource set and  $n$  is the total number of units in the set. Niche width is maximized ( $B = 1.0$ ) for a species that uses all resource units equally. For example, a sap-feeder which is equally abundant in all grass zones would be broad-niched with regard to the microhabitat distribution in the grass system and yield a  $B$  value of 1.0. On the other hand, a specialist that occurred only in the thatch zone would be relatively narrow-niched and possess a  $B$  value much less than 1.0.

The similarity in resource exploitation among sap-feeding species was calculated using the formula:

$$O_{ij} = 1.0 - 0.5 \sum_{h=i}^n |p_{ih} - p_{jh}|$$

where  $O_{ij}$  is the percent similarity or overlap and  $P_{ih}$  and  $P_{jh}$  are the proportions of species  $i$  and  $j$  associated with the resource category  $h$  (Schoener 1970, also see Rathcke 1976). This formula (Schoener 1970) and Southwood's (1966) percentage of similarity are equivalent methods for calculating overlap. Like niche width ( $B$ ), this measure is also constrained between 0 and 1.0. Because my emphasis is on the difference rather than similarity in the way species use resources, I have subtracted  $O_{ij}$  from 1.0 and used the remainder as an index of niche difference.

#### RESULTS

Seven resident species of sap-feeding insects regularly occurred on *S. patens*. Of these, four were plant-

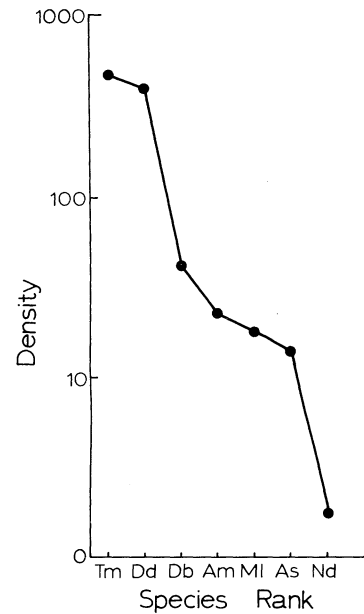


FIG. 1. Density (mean number of individuals per kilogram of *S. patens*) of sap-feeder species on *S. patens* ranked in order of decreasing abundance. Tm = *Tumidagena minuta*, Dd = *Delphacodes detecta*, Db = *Destria bisignata*, Am = *Amplicephalus simplex*, Ml = *Megamelus lobatus*, As = *Aphelonema simplex*, Nd = *Neomegamelanus dorsalis*. Data from Raup and Denno (1979).

hoppers (Delphacidae), *Delphacodes detecta* (Van Duzee), *Neomegamelanus dorsalis* (Metcalf), *Tumidagena minuta* McDermott, and *Megamelus lobatus* Beamer, and two were leafhoppers (Cicadellidae), *Amplicephalus simplex* (Van Duzee) and *Destria bisignata* (Sanders and DeLong). There was also a fulgoroid (Issidae), *Aphelonema simplex* (Uhler). The relative abundances of the seven sap-feeders in the community are shown in Fig. 1. Two other leafhoppers and the stink bug *Rhytidolomia saucia* (Say) were residents, but they are omitted from this analysis because of their rarity (see Denno 1977).

#### Microhabitat distribution of sap-feeders

Four of the sap-feeders, *D. detecta*, *N. dorsalis*, *A. simplex* and *Am. simplex* occurred primarily in the upper stratum (zones three through five) of the grass system above the thatch layer (Fig. 2). Niche overlap values ( $O_{ij}$ ) among this complement of four species were high for the microhabitat dimension (outlined area A in Table 1). However, within the upper stratum there were subtle but consistent differences in their distributions. *D. detecta* occurred abundantly in zones three through five, but was most common on the upright terminal vegetation. Also, it was the only species observed feeding on the seed heads of the grass. *N. dorsalis* was similarly distributed, but fed mostly on subterminal and terminal blades. *A. simplex* occurred

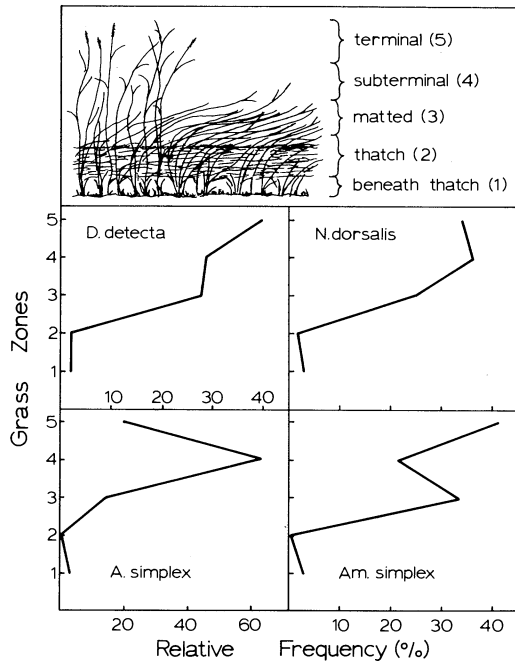


FIG. 2. Microhabitat partitioning. Relative frequency of *D. detecta*, *N. dorsalis*, *A. simplex*, and *Am. simplex* in terminal (5), subterminal (4), matted (3), thatch (2), and beneath thatch (1) zones of *S. patens*.

predominantly in the shaded subterminal layer and showed the highest degree of microhabitat specialization of these four residents of the upper stratum. The relatively small microhabitat niche width value (.436) of *A. simplex* reflects its restricted distribution (Table 2). *Am. simplex* was most abundant on vegetation that was in direct sun; it did not seem to matter whether the grass was upright or matted.

A second group of three species, *T. minuta*, *M. lobatus* and *D. bisignata*, inhabited primarily the lower

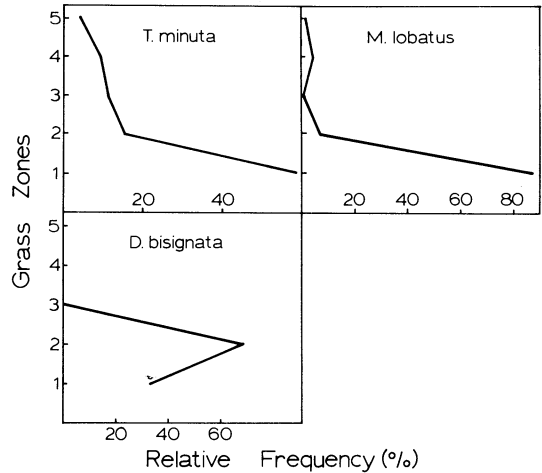


FIG. 3. Microhabitat partitioning. Relative frequency of *T. minuta*, *M. lobatus*, and *D. bisignata* in terminal (5), subterminal (4), matted (3), thatch (2), and beneath thatch (1) zones of *S. patens*.

stratum of the grass, in and beneath the thatch layer (zones one and two) (Fig. 3) and niche overlap values among this group of species were high (outlined area B in Table 1). Of the three species, all but *D. bisignata* inhabited the open area beneath the thatch where they were associated with the crowns and tillers of the grass. *D. bisignata* was the only member of the sap-feeding guild to exploit heavily the thatch layer. Apparently, this leafhopper is small enough to negotiate the dense thatch zone, yet has the mouthparts necessary to penetrate the tough dead sheaths that surround the grass culms. Although *T. minuta* was most abundant beneath the thatch, it was not unusual for it to venture upward into other zones. If disturbed it would quickly descend into the grass. This behavior, however, was never observed in *M. lobatus*, a plant-hopper which rarely left the confines beneath the

TABLE 1. Overlap ( $O_{ij}$ ) in the microhabitat distributions of sap-feeders inhabiting the *S. patens* grass system. Dd = *Delphacodes detecta*, Nd = *Neomegamelanus dorsalis*, Ams = *Amplicephalus simplex*, As = *Aphelonema simplex*, Tm = *Tumidagena minuta*, MI = *Megamelus lobatus*, and Db = *Destria bisignata*.

Species	Dd	Nd	Ams	As	Tm	MI	Db
Dd	1.000						
Nd	.914	1.000					
Ams	.908	.830	1.000				
As	.640	.727	.576	1.000			
Tm	.286	.290	.274	.279	1.000		
MI	.100	.106	.089	.094	.727	1.000	
Db	.040	.045	.028	.034	.489	.401	1.000

NOTE: A = upper, B = lower and C = between-strata comparisons.

TABLE 2. Relative niche width (B) of sap-feeders with respect of their microhabitat, seasonal and elevational distributions in *S. patens*. Species code as in Table 1.

Resource dimension	Species						
	Dd	Nd	Ams	As	Tm	MI	Db
Microhabitat	.632	.640	.596	.436	.493	.261	.359
Season*	.355 (3)	.409 (3)	.249 (1)	.428 (2)	.409 (2)	.381 (2)	.313 (2)
Elevation	.757	.224	.720	.679	.482	.766†	.855

NOTE: \* = Numbers in parentheses indicate the number of generations per year.

† = Calculated on D-vac collected insects.

thatch. As a group, the species of the lower stratum had more restricted distributions in the grass system compared to those in the upper stratum. Consequently, niche width (B) values for the microhabitat dimension were generally low (Table 2).

#### Seasonal distribution of sap-feeders

For the most part, residents of the upper stratum had very similar seasonal distributions (left column of Fig. 4) resulting in generally high overlap values (outlined area A in Table 3). For *D. detecta*, *N. dorsalis* and *A. simplex*, populations began increasing in May, peaked in September, and then decreased rapidly. Only *Am. simplex*, a univoltine species, peaked earlier in the season, during July. For more detailed information on the phenology of the various sap-feeders, see Denno (1977).

*T. minuta*, *M. lobatus*, and *D. bisignata*, all lower stratum residents, also showed very similar seasonal distributions (right column of Fig. 4) and high overlap values (outlined area B in Table 3). Compared to the upper stratum species, lower stratum sap-feeders delay their phenology about 1 mo. Populations increased in June, peaked during October and then declined rapidly. The seasonal displacement between upper and lower strata species resulted in higher average overlap values among sap-feeders inhabiting the same stratum (mean  $O_{ij}$  = .631 and .692 for upper and lower strata

species, respectively) than for sap-feeders in different strata (mean  $O_{ij}$  for species in outlined area C of Table 3 = .440).

There was a tendency toward specialization along the seasonal dimension by some of the sap-feeders. Univoltine species occurred only in the upper stratum (*Am. simplex*), bivoltine species inhabited both strata and trivoltine species (*D. detecta* and *N. dorsalis*) were limited to the upper stratum (Table 2). Although seasonal niche width values (Table 2) are significantly correlated with the number of generations per year ( $r = .712, P < .05$ ), they do not reflect the generational difference between upper and lower strata residents.

#### Elevational distribution of sap-feeders

All sap-feeders but *N. dorsalis* were most abundant on patches of *S. patens* that occurred from  $\approx$ MHW to 10 cm above (Figs. 5 and 6) and moderate to high elevational overlap values were recorded among these six species (Table 4). Only *N. dorsalis* predominated on, and was for the most part restricted to, patches at the upper end of the elevational range of the grass. Consequently, habitat overlap was small between *N. dorsalis* and all other species. Upper stratum species partitioned the elevational habitat dimension more than did lower stratum species. Mean elevational overlap values for species of the upper and lower strata (outlined areas A and B in Table 4) were .457

TABLE 3. Overlap ( $O_{ij}$ ) in the seasonal distributions of sap-feeders in *S. patens*. Species code as in Table 1.

Species	Dd	Nd	Ams	As	Tm	MI	Db
Dd	1.000						
Nd	.875	1.000					
Ams	.403	.446	1.000				
As	.802	.764	.496	1.000			
Tm	.559	.556	.311	.526	1.000		
MI	.462	.463	.099	.444	.674	1.000	
Db	.602	.506	.142	.611	.726	.676	1.000

NOTE: Mean seasonal niche overlap values for group A (upper stratum comparisons), B (lower stratum comparisons) and C (between-strata comparisons) species are .631, .440 and .692 respectively.

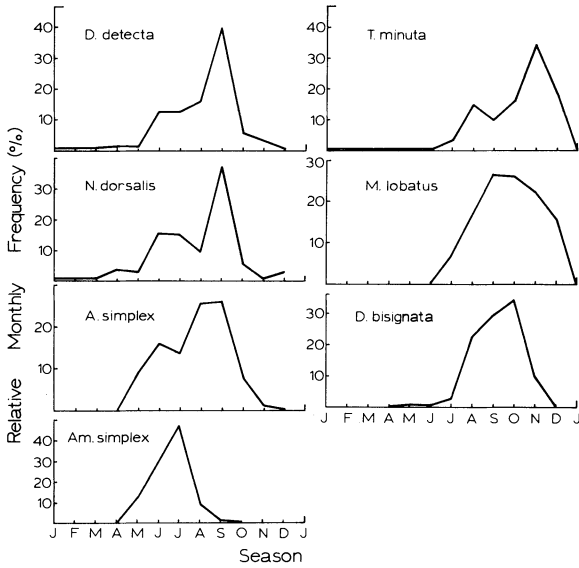


FIG. 4. Seasonal partitioning. Relative monthly frequency of sap-feeders on *S. patens*.

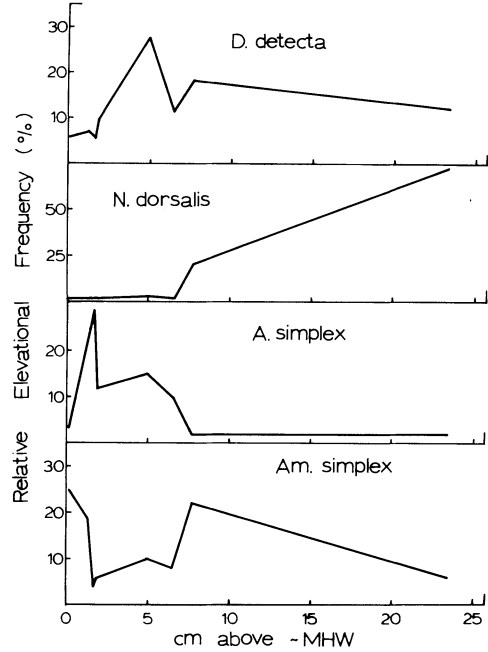


FIG. 5. Elevational partitioning. Relative elevational frequency of *D. detecta*, *N. dorsalis*, *A. simplex*, and *Am. simplex* on patches of *S. patens* along a gradient from  $\approx$ MHW to 25 cm above.

and .634, respectively. The smaller mean overlap for the upper stratum group of species is partly attributable to comparisons of *D. detecta*, *Am. simplex*, and *A. simplex* with *N. dorsalis*, but there was also moderate partitioning among the other species as well. The average overlap between species of the upper and lower strata (outlined area C in Table 4) was .573.

Niche width values suggest that except for *N. dorsalis* and *T. minuta*, sap-feeders are relatively wide-niched with respect to grass elevation (Table 2). In reality, niche width values are probably an overestimate for some of the species. An unavoidable spacing error was committed because seven of the eight grass patches sampled occurred between  $\approx$ MHW and 10 cm above, while only one patch occurred between 10 and 25 cm above MHW (see Colwell and Futuyma 1971).

Had grass patches of the appropriate size been available between 10 and 25 cm above MHW, allowing for equitable sampling along the elevational gradient, the niche width values of several species (e.g., *A. simplex*, *T. minuta*, and *M. lobatus*) would undoubtedly be less.

*Relative importance of niche and habitat dimensions*

Schoener (1974) defines important dimensions as those which serve to separate some minimal percentage of species pairs. Therefore, dimensions can be

TABLE 4. Overlap ( $O_{ij}$ ) in the elevational distribution of sap-feeders in *S. patens*. Species code as in Table 1.

Species	Dd	Nd	Ams	As	Tm	MI	Db
Dd	1.000						
Nd	.404	1.000					
Ams	.648	.334	1.000				
As	.647	.124	.586	1.000			
Tm	.762	.247	.510	.578	1.000		
MI	.561	1.99	.766	.723	.563	1.000	
Db	.794	.342	.643	.753	.700	.640	1.000

NOTE: Mean elevational overlap values for group A (upper stratum comparisons), B (lower stratum comparisons) and C (between-strata comparisons) species are .457, .634, and .573, respectively.

TABLE 5. Ecological differences ( $1 - O_{ij}$ ) between species pairs along three ecotope dimensions. Species code as in Table 1.

Species pairs	Season	Elevation	Microhabitat
Dd-Nd	.12	.60*	.09
Dd-Tm	.44	.24	.71*
Dd-Ml	.54	.44	.90*
Dd-Ams	.60*	.35	.09
Dd-Db	.40	.21	.96*
Dd-As	.20	.35	.36*
Nd-Tm	.44	.75*	.71
Nd-Ml	.54	.80	.89*
Nd-Ams	.55	.67*	.17
Nd-Db	.49	.66	.96*
Nd-As	.24	.88*	.27
Tm-Ml	.33	.44*	.27
Tm-Ams	.69	.49	.73*
Tm-Db	.27	.30	.51*
Tm-As	.47	.42	.72*
Ml-Ams	.90	.23	.91*
Ml-Db	.32	.36	.60*
Ml-As	.56	.28	.91*
Ams-Db	.86	.36	.97*
Ams-As	.50*	.41	.42
Db-As	.39	.25	.97*
$\bar{x} \pm \sigma$	.47 $\pm$ .19	.45 $\pm$ .19	.62 $\pm$ .30

\* = Dimension that best separates the species pair.

ranked in importance according to the number of species pairs that are best separated by each dimension. The amount of ecological separation was determined for each pair of sap-feeders along each dimension by subtracting overlap values from one ( $1 - O_{ij}$ ) (Table 5). Of the 21 pairs of sap-feeders, 14 were best separated by the microhabitat dimension, while the elevational and seasonal dimensions best separated 5 and 2 pairs, respectively. If the three dimensions were equally partitioned, one would expect each to account for the greatest amount of separation for one-third of the 21 interactions or 7 times. The observed pattern (14, 5, 2) is significantly different from an expected pattern of equal partitioning when tested with a  $\chi^2$

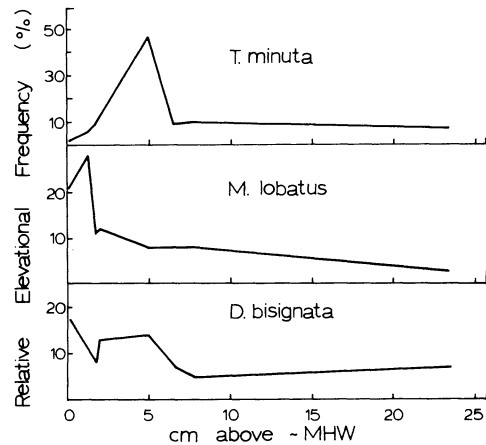


FIG. 6. Elevational partitioning. Relative elevational frequency of *T. minuta*, *M. lobatus*, and *D. bisignata* on patches of *S. patens* along a gradient from  $\approx$ MHW to 25 cm above.

goodness of fit test ( $\chi^2 = 11.143, P < .01$ ). Also, the average (mean of 21 pairs) ecological separation for the microhabitat, seasonal and elevational dimensions was .62, .47, and .45, respectively. The data strongly suggest that sap-feeders partition the microhabitat niche dimension far more than the seasonal niche and elevational habitat dimensions.

*Interspecific competition*

MacArthur (1972) estimates the precariousness of competitors in a community by the relationship of  $d$ , the distance between the means of the distributions of two species along a resource coordinate, and  $\sigma_1$  and  $\sigma_2$ , their standard deviations. He reasons that if  $d$  is much less than  $\sqrt{\sigma_1^2 + \sigma_2^2}$ ,  $\alpha$  (competition coefficient) is near 1, and the two species use the resource too similarly to coexist. If  $d > \sqrt{\sigma_1^2 + \sigma_2^2}$ , competition is potentially reduced to a point where coexistence becomes possible. Although this type of

TABLE 6. The precariousness of sap-feeders ( $d/\sqrt{\sigma_1^2 + \sigma_2^2}$ ) along the microhabitat dimension. If  $d/\sqrt{\sigma_1^2 + \sigma_2^2} > 1$ , competition is potentially reduced to a point where coexistence becomes possible. Species code as in Table 1.

Species	Dd	Nd	Ams	As	Tm	Ml	Db
Dd	0						
Nd	.033	0					
Ams	.024	.008	0				
As	.43	.006	.015	0			
Tm	1.416	1.395	1.372	1.481	0		
Ml	2.158	2.143	2.082	2.357	.383	0	
Db	2.186	2.170	2.086	2.499	.127	.415	0

NOTE: C = between-strata comparisons.

TABLE 7. The precariousness of sap-feeders ( $d/\sqrt{\sigma_1^2 + \sigma_2^2}$ ) along the seasonal niche dimension. If  $d/\sqrt{\sigma_1^2 + \sigma_2^2} > 1$ , competition is potentially reduced to a point where coexistence becomes possible. Species code as in Table 1.

Species	Dd	Nd	Ams	As	Tm	MI	Db
Dd	0						
Nd	.144	0					
Ams	.811	.493	0				
As	.142	.026	.681	0			
Tm	.377	.471	1.222	.936	0		
MI	.942	.956	2.160	1.142	.492	0	
Db	.614	.674	1.922	.818	.146	.451	0

NOTE: A = upper, B = lower and C = between-strata comparisons.

analysis certainly has its shortcomings, and MacArthur (1972) and Schoener (1974) discuss some of them, it theoretically allows for a precise definition of just how much overlap in resource use is permitted between two competitors.

The results of a  $d/\sqrt{\sigma_1^2 + \sigma_2^2}$  analysis performed on all pairwise combinations of the seven sap-feeders for the microhabitat, elevational and seasonal dimensions, corroborate in large part the implications of the niche overlap ( $O_{ij}$ ) analyses (Tables 1, 3 and 4). The magnitude of all microhabitat overlap values between the upper and lower zone species (outlined area C of Table 1) is sufficiently low to permit coexistence ( $d/\sqrt{\sigma_1^2 + \sigma_2^2} > 1$  for all between-strata comparisons; see area C in Table 6).

No within-stratum species pairs differed sufficiently along the seasonal niche dimension (outlined areas A and B in Table 7). Several  $d/\sqrt{\sigma_1^2 + \sigma_2^2}$  values are  $>1$  for between-strata comparisons (outlined area C of Table 7), but from a competitive point of view these high values are probably irrelevant because interactions between the residents in the upper and lower grass strata are minimal. Also, the  $d/\sqrt{\sigma_1^2 + \sigma_2^2}$  analysis suggests that the overlap of only *N. dorsalis* with other sap-feeders along the elevational habitat dimension is sufficiently low to allow for coexistence (compare Tables 4 and 8).

*Body weight relationships of sap-feeders*

Hutchinson (1959) measured the feeding apparatus of closely related species when they were sympatric and allopatric. He found that the ratio of the largest to the smallest dimension was  $\approx 1.0$  when the species were allopatric, but where they co-occurred the species differed by a factor of 1.2–1.4. He concluded that a difference of about 1.2–1.4 was necessary for the two congeners to coexist, and subsequent work has tended to support this conclusion. For example, Rosenzweig and Sterner (1970) and Brown (1975) suggested that coexistence in heteromyid rodent communities is permitted by body size (mass) differentials.

Similarly, various sizes of sap-feeders may be able to negotiate the microhabitat in different ways, and oviposition, feeding and hiding sites that are available to a small species may not be to a larger one. Consequently, sap-feeders that differ in size may use resources differently and thereby, reduce competition. I used a body size ratio of 1.3 (mean of Hutchinson's 1.2–1.4 range) as a measure of the difference necessary to permit coexistence.

The mean adult body mass of the various *S. patens* sap-feeders ranged from 0.11 to 0.78 mg (Table 9). When the entire assemblage was considered as a unit, three species pairs (*M. lobatus* and *D. detecta*, *D. detecta* and *D. bisignata*, and *A. simplex* and *Am. simplex* failed to differ in body weight by a factor of at least 1.3 (Ratio A of Table 9). However, when species were grouped by microhabitat into upper and lower zone residents (Ratio B and C, respectively, of Table 9) only *A. simplex* and *Am. simplex* differed by a ratio (1.15) less than 1.30.

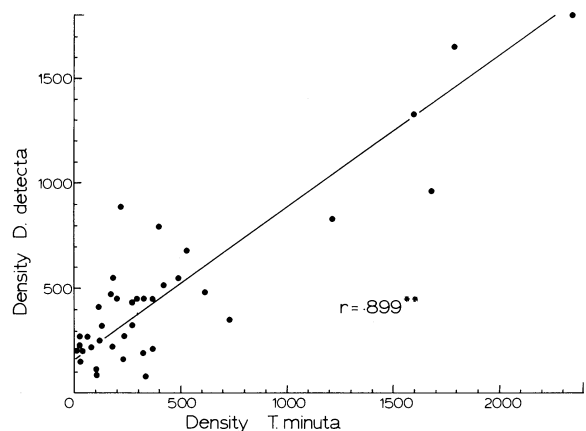


FIG. 7. Relationship between the densities of *D. detecta* and *T. minuta* in samples taken during July 1976 in patches of *S. patens* that occur within 10 cm of MHW.



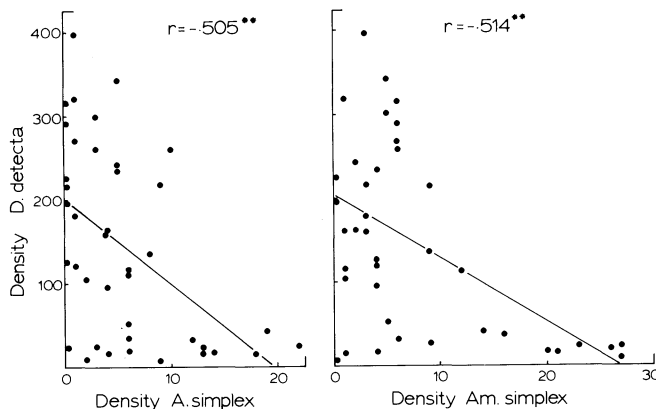


FIG. 8. Relationship between the density of *D. detecta* and the densities of *A. simplex* and *Am. simplex* in samples taken during May 1976 in patches of *S. patens* that occur within 10 cm of MHW.

*Density relationships of some sap-feeders*

There is a positive relationship ( $r = .899, P < .01$ ) between the densities of *D. detecta*, the upper stratum dominant, and *T. minuta*, the lower stratum dominant, in samples taken during July when these species are both common (Fig. 7). Thus, there is no apparent negative effect of one of these species on the other. This is not surprising when one considers that they occupy different strata and rarely encounter one another.

When occupants of the same stratum are considered, the pattern is quite different. There are negative relationships ( $r = -.505, P < .01$  and  $r = -.514, P < .01$ , respectively) between the densities of *A. simplex*, *Am. simplex*, and *D. detecta* (Fig. 8). The regressions were generated on the basis of samples taken in May when the nymphs of *A. simplex* and *Am. simplex* (adult size is large compared to *D. detecta*) occur with the adults of *D. detecta* and when body sizes of the three species are similar. Also, there is a negative relationship ( $r = -.379, P < .05$ ) between the densities of *A. simplex* and *Am. simplex*, two very similar-sized

species that commonly co-occur as adults during July (Fig. 9).

DISCUSSION

During the summers of 1974–1976, in the Tuckerton area, populations of sap-feeding insects on large patches (> 1 ha) of *S. patens* were high and the grass showed definite signs of deterioration by July. Grass plants were heavily punctured from feeding and oviposition resulting in chlorotic leaf blades that yellowed from tip to axil as the season progressed. Large patches of yellow vegetation were mixed in with others that showed less damage. Thus, resources appear to be limiting in certain years and probably over periods of several years as well, allowing for the frequent development of an equilibrium community of sap-feeders. Under these circumstances competition among the various sap-feeders for resources is likely and selection should favor differences in resource utilization.

I examined resource partitioning along one habitat

TABLE 8. The precariousness of sap-feeders ( $d/\sqrt{\sigma_1^2 + \sigma_2^2}$ ) along the elevational habitat dimension. If  $d/\sqrt{\sigma_1^2 + \sigma_2^2} > 1$ , competition is potentially reduced to a point where coexistence becomes possible. Species code as in Table 1.

Species	Dd	Nd	Ams	As	Tm	MI	Db
Dd	0						
Nd	1.163	0					
Ams	.331	1.569	0				
As	.560	1.837	.224	0			
Tm	.187	1.434	.163	.412	0		
MI	.554	1.847	.228	.018	.408	0	
Db	.134	1.282	.181	.390	.037	.390	0

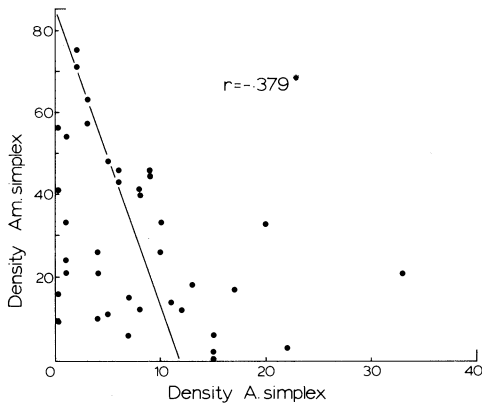


FIG. 9. Relationship between the densities of *Am. simplex* and *A. simplex* in samples taken during July 1976 in patches of *S. patens* that occur within 10 cm of MHW.

(elevation) and two niche dimensions (microhabitat and season) for seven sap-feeders occurring on *S. patens*. Of the three dimensions, the microhabitat dimension was best partitioned, accounting for the most separation among the seven sap-feeders. This is consistent with the general observation of Schoener (1974) that segregation by food-type is more important for animals feeding on food that is large in relation to their own size than it is for animals feeding on relatively small food items. He cites herbivorous insects that spend most of their lives on single plant parts as an example. Four species: *Delphacodes detecta*, *Neomegamelanus dorsalis*, *Aphelonema simplex*, and *Amplicephalus simplex* occurred primarily above the thatch layer in the upper stratum of their host grass. Another three species, *Tumidagena minuta*, *Megamelus lobatus*, and *Destria bisignata* existed within and beneath the thatch in the lower stratum. There was evidence for further microhabitat partitioning

TABLE 9. Adult dry body mass (mg) and body mass ratios (large species/small species) for the resident sap-feeders on *S. patens*.

Species	Dry mass ( $\bar{x} \pm \sigma$ )	Ratio A	Ratio B	Ratio C
<i>N. dorsalis</i>	.11 ± .008	1.36	2.73	1.67
<i>T. minuta</i>	.15 ± .018			
<i>M. lobatus</i>	.25 ± .032	1.67		
<i>D. detecta</i>	.30 ± .037	1.20		1.36
<i>D. bisignata</i>	.34 ± .012	1.13		
<i>A. simplex</i>	.68 ± .036	2.00		2.27
<i>Am. simplex</i>	.78 ± .044	1.15	1.15	

NOTE: Ratios between all species (A), upper stratum species (B) and lower stratum species (C).

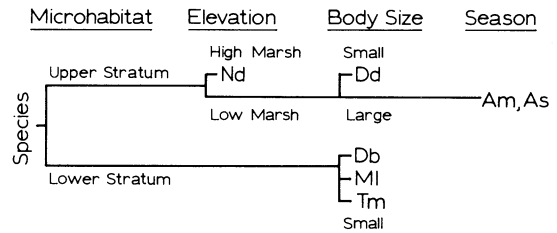


FIG. 10. Niche differentiation in the guild of *S. patens* sap-feeders. Branching under microhabitat and elevational dimensions indicates that there is sufficient resource partitioning ( $d > \sqrt{\sigma_1^2 + \sigma_2^2}$ ) to permit coexistence. Branching under the body size category indicates that sap-feeders differ sufficiently in body size (ratio of large to small species >1.3) to coexist. Species code as in Fig. 1.

among upper and lower strata species. For instance, *D. detecta* feeds on seed heads, but the other upper stratum species do not. Of the lower stratum residents, only *D. bisignata* feeds within the thatch, and the others remain beneath.

There was very little elevational separation among the sap-feeders where three upper and all lower strata species occurred most abundantly within 10 cm of MHW level. One upper stratum species, *N. dorsalis*, predominated on the upland fringe of *S. patens* where it displaced the remainder of the subguild. Consequently, the habitat (elevational) dimension was partitioned far less than the food-type (microhabitat) dimension. This result is not consistent with the general observation of Schoener (1974) that habitat dimensions are important more often than food-type dimensions. Nutrient subsidy from tidewaters is higher at the lower end of the elevational range of *S. patens*, resulting in more vigorous plants there (Blum 1968). Apparently, selective pressures associated with resource quality have placed a premium on feeding near MHW level for most sap-feeders.

The seasonal niche dimension was also poorly partitioned. Upper stratum residents have very similar phenologies with only *Am. simplex* occurring a bit earlier in the season. The lower stratum species also shared very similar phenologies. In the Mid-Atlantic states, the perennial *S. patens* sprouts in April, attains maximum live standing crop during July or early August and thereafter slowly senesces (Busch 1975). There are probably nutrient advantages to be gained for all species by beginning to feed early in the season on the succulent growing grass, and selective pressures associated with resource quality probably best explain the relative synchrony of the seasonal distributions of sap-feeders.

Schoener (1974) also observes that temporal dimensions are often less important than food-type dimensions. However, the abundance of lower stratum species peaked about 1 mo later than the abundance of upper stratum residents and trivoltine species oc-

curred only in the upper stratum. Blum (1968) documents the slow warming of the marsh surface under the thatch of *S. patens* in spring. Cooler spring temperatures under the thatch layer are probably responsible for the observed (1 mo) delay in the development of lower stratum species and for constraining to two the number of annual generations a sap-feeder can obtain. The body size of lower stratum leafhoppers and planthoppers was generally smaller compared to upper stratum species. The three lower stratum species all weighed less than 0.5 mg (adult mass), while two of the four upper stratum species weighed more than 0.5 mg. Apparently, by reducing body size, and consequently generation time, lower stratum species are able to cope with the cooler temperatures incurred beneath the thatch.

Body size differences may be important in other ways as well. For instance, small species like *N. dorsalis* (0.11 mg) and *D. detecta* (0.30 mg) can exploit the most terminal part of a leaf blade, while larger species like *A. simplex* (0.68 mg) are too large to negotiate such structures. Even though *Am. simplex* (0.78 mg) appears to be relatively more abundant than *N. dorsalis* (0.11 mg) on terminal vegetation (Fig. 2), it remains on the larger culms and blades in this zone and never ventures out to the narrow tips as does *N. dorsalis*. By feeding in small microhabitats, a small species can avoid competing with larger species which presumably have greater competitive ability (see Miller 1967, Van Valen 1973, Price 1975, and Morse 1977). Consequently, body size differences probably allow for further microhabitat partitioning within a particular grass stratum. The body weights of the seven leafhoppers and planthoppers ranged from 0.11 mg (*N. dorsalis*) to 0.78 mg (*Am. simplex*). Body size ratios (large/small) differed by more than the 1.3 ratio proposed by Hutchinson (1959) for all within-stratum species pairs except *A. simplex* and *Am. simplex*. Furthermore, body size ratios for species in the same stratum (see ratios B and C in Table 6) get smaller as body size increases. Contrarily, Schoener (1965, 1974) and May and MacArthur (1972) suggest that to hold competition below a certain intensity, larger species must space more widely on a body size axis. This can stem from the likelihood that large species feed on large food items that are often rare (Schoener and Janzen 1968) and have to maintain a greater size difference in order to sustain a viable population size (Schoener 1965). More important, large species usually eat a greater range of food sizes than small ones, probably because their optimal food is relatively rare (Schoener 1974). Consequently, increased variance in food size creates a greater potential for niche overlap and large species should maintain a greater size difference along a size axis in order to coexist (Schoener 1974).

With this guild of sap-feeders however, it appears that small species exploit a greater range of resources than large ones. For instance, the microhabitat niche

breadths of *D. detecta* and *T. minuta*, the smallest species over most of the elevational range of *S. patens*, are larger than the breadth values for all other species in the same (upper or lower) stratum (see Table 2). *N. dorsalis* also follows this pattern on the high marsh. Under these circumstances where small species have an increased variance in the food resources they exploit (e.g., *D. detecta* feeds on apical and basal portions of leaf blades, stems and seed heads in terminal, subterminal and matted layers of grass), the body size ratios of neighboring species on the size axis should be greater than for larger species with more specialized resource requirements. This is precisely what occurs in the *S. patens* sap-feeder guild.

Based on MacArthur's (1972  $d > \sqrt{\sigma_1^2 + \sigma_2^2}$ ) analysis that estimates the probability for competitive exclusion along resource dimensions, and Hutchinson's (1959) ratio of  $\approx 1.3$  as an indication of the amount of morphological (body size in this case) difference necessary to permit coexistence, all species but two (*Am. simplex* and *A. simplex*) differ enough in the way they use *S. patens* to allow for co-occurrence (Fig. 10). The sap-feeders segregate well into two sub-guilds (upper and lower strata species) along the microhabitat dimension. Of the lower stratum species none are separated by the elevational dimension, but all differ in body size by a ratio  $> 1.3$ , implying that coexistence is possible. *N. dorsalis* displaces the other upper stratum species on the elevational dimension. The body size of *D. detecta* is sufficiently small to separate it from *Am. simplex* and *A. simplex*. However, *A. simplex* and *Am. simplex* are not sufficiently different from one another along any niche or habitat dimensions, nor do they differ in body size by a factor  $> 1.3$ .

Realizing that the above analyses are only indices of the precariousness of a species in a community, the question still remains as to how *Am. simplex* and *A. simplex* both persist in the guild when they use resources so similarly. Their position seems even more precarious (see Schoener 1974) when one considers that their smaller instars are very similar in size to the larger nymphs and adults of *D. detecta*, creating a situation where competition is potentially further intensified. The significant negative relationship between the densities of both *A. simplex* and *Am. simplex* and *D. detecta* in samples taken on grass patches within 10 cm of MHW during late May (Fig. 8) and *A. simplex* and *Am. simplex* during July (Fig. 9) is consistent with the argument that these upper stratum species compete.

Hutchinson (1953) suggests that if there is a tendency for competitively weaker species to disperse more easily, then coexistence is possible where catastrophic events destroy previously occupied habitats while creating new empty sites. Similarly, Skellam (1951) hypothesizes that if species with lower reproductive rates also have high dispersal rates, then coexistence

is possible. Evidence suggests that the leafhopper, *Am. simplex*, is able to coexist in the guild by employing just such a fugitive tactic. For instance, of the seven sap-feeders, *Am. simplex* is the only species that has fully developed wings and retains the ability to fly. Denno (1977) documents its excellent ability to colonize defaunated plots of *S. patens*. Contrarily, *D. detecta*, *N. dorsalis*, *M. lobatus*, *T. minuta*, and *A. simplex* exhibit wing-dimorphism (produce both flightless brachypters and macropters that fly) and Tuckerton populations contain 86, 88, 97, >99, >99% of the flightless morph, respectively (Denno 1976, 1978). Also, *D. bisignata* is sexually dimorphic, where males are macropterous and females brachypterous.

The configuration of *S. patens* on the salt marshes of the Mid-Atlantic states appears to provide a resource situation that allows for the survival of the fugitive leafhopper, *Am. simplex*. *S. patens* occurs as a mosaic of different-sized patches interrupted by *S. alterniflora*. Raupp and Denno (1979) propose that removal rates of sap-feeders are greater in small ( $\approx 1$  ha) compared to large ( $\approx 20$  ha) patches because the sporadic effects of storm tides are stronger there. The fact that sap-feeder loads (individuals per kilogram of grass) are greater on large patches is consistent with this hypothesis. Thus, tidewaters catastrophically reduce populations of sap-feeders more frequently on small patches, creating relatively vacant sites. I suggest that of the seven sap-feeders *Am. simplex* is best able to find and exploit small patches of *S. patens*.

Lastly, in the *S. patens* guild of sap-feeders, potential competitive interactions are minimized primarily by microhabitat partitioning and body size differences that probably further increase niche differentiation. The one leafhopper, *Am. simplex*, that shares a niche very similar to *A. simplex* and appears to occupy a rather precarious position in the guild, is unique because it is an excellent colonizer and apparently able to locate relatively vacant or more favorable sites, thereby allowing coexistence.

#### ACKNOWLEDGMENT

I gratefully acknowledge Barbara Denno for processing and counting some of the samples, David Inouye, Mark McClure, and Larry Pinto for their helpful comments on the manuscript, and Tina Middlebrook for typing the final draft. This is Scientific Article Number A2555, Contribution Number 5589, of the Maryland Agricultural Experiment Station, Department of Entomology.

#### LITERATURE CITED

- Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* **44**:445-456.
- Andrzejewska, L. 1965. Stratification and its dynamics in meadow communities of Auchenorrhyncha (Homoptera). *Ekologia Polska, Seria A* **13**:686-715.
- Blum, J. L. 1968. Salt marsh spartinas and associated algae. *Ecological Monographs* **38**:199-221.
- Brown, J. H. 1975. Geographical ecology of desert rodents. Pages 315-341 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, USA.
- Busch, D. A. 1975. The failure of temefos and chlorpyrifos to affect the short-term productivity of *Spartina alterniflora* and *S. patens* on a New Jersey salt marsh. *Proceedings of the New Jersey Mosquito Extermination Association* **62**:50-55.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**:567-576.
- Davis, L. V., and I. E. Gray. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. *Ecological Monographs* **36**:275-295.
- Denno, R. F. 1976. Ecological significance of wing-polymorphism in Fulgoroidea which inhabit tidal salt marshes. *Ecological Entomology* **1**:257-266.
- . 1977. Comparison of the assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in the genus *Spartina*. *Environmental Entomology* **6**:359-371.
- . 1978. The optimum population strategy for plant-hoppers (Homoptera:Delphacidae) in stable marsh habitats. *Canadian Entomologist* **110**:135-142.
- Denno, R. F., and E. E. Grissell. 1979. The adaptiveness of wing-dimorphism in the salt marsh inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae) *Ecology* **60**:221-236.
- Duncan, W. H. 1974. Vascular halophytes of the Atlantic and Gulf coasts of North America north of Mexico. Pages 23-50 in R. J. Reibold and W. H. Queen, editors. *Ecology of halophytes*. Academic Press, New York, New York, USA.
- Halkka, O., M. Raatikainen, L. Halkka, and T. Raatikainen. 1977. Coexistence of four species of spittle-producing Homoptera. *Annales Zoologici Fennici* **14**:228-231.
- Hatcher, B. G., and K. H. Mann. 1975. Above-ground production of marsh cordgrass (*Spartina alterniflora*) near the northern end of its range. *Journal of the Fisheries Research Board of Canada* **32**:83-87.
- Hutchinson, G. E. 1953. The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* **105**:1-12.
- . 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* **93**:145-159.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. H. 1972. *Geographical ecology—patterns in the distribution of species*. Harper and Row, London, England.
- May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences (USA)* **69**:1109-1113.
- McClure, M. S. 1974. Biology of *Erythroneura lawsoni* (Homoptera:Cicadellidae) and coexistence in the sycamore leaf-feeding guild. *Environmental Entomology* **3**:59-68.
- McClure, M. S., and P. W. Price. 1975. Competition and coexistence among sympatric *Erythroneura* leafhoppers (Homoptera:Cicadellidae) on American sycamore. *Ecology* **56**:1388-1397.
- McClure, M. S., and P. W. Price. 1976. Ecotype characteristics of coexisting *Erythroneura* leafhoppers (Homoptera:Cicadellidae) on sycamore. *Ecology* **57**:928-940.
- Miller, R. S. 1967. Pattern and process in competition. *Advances in Ecological Research* **4**:1-74.
- Mobberley, D. G. 1956. Taxonomy and distribution of the genus *Spartina*. *Journal of Science of Iowa State College* **30**:471-574.
- Morse, D. H. 1977. Resource partitioning in bumble bees: The role of behavioral factors. *Science* **197**:678-680.
- Price, P. W. 1975. *Insect ecology*. John Wiley and Sons, New York, New York, USA.

- Rathcke, B. J. 1976. Competition and coexistence within a guild of herbivorous insects. *Ecology* 57:76-87.
- Raupp, M. J., and R. F. Denno. 1979. The influence of patch size on a guild of sap-feeding insects that inhabit the salt marsh grass *Spartina patens*. *Environmental Entomology* 8:412-417.
- Redfield, A. C. 1972. Development of a New England salt marsh. *Ecological Monographs* 42:201-237.
- Rosenzweig, M. L., and P. Sterner. 1970. Population ecology of desert rodent communities: body size and seed husking as bases for heteromyid coexistence. *Ecology* 51:217-224.
- Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189-213.
- . 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408-418.
- . 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Schoener, T. W., and D. H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *American Naturalist* 102:207-224.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196-218.
- Southwood, T. R. E. 1966. *Ecological methods*. Methuen, London, England.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 4:614-624.
- Van Valen, L. 1973. Body size and numbers of plants and animals. *Evolution* 27:27-35.
- Webb, D. P. 1976. Edge effects on salt marsh arthropod community structures. *Journal of the Georgia Entomology Society* 11:17-27.
- Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat and ecotone. *American Naturalist* 107:321-338.