ECOTOPE DIFFERENTIATION IN A GUILD OF SAP-FEEDING INSECTS ON THE SALT MARSH GRASS, SPARTINA PATENS

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 leaf-hoppers 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 Aphelionema 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)
and two niche factors (microhabitat distribution within
the grass system and temporal utilization) (see Whit-
taker 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 par-
tioned 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 (Mobber-
ley 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 com-
monly mixed in with other halophytic plants (Mob-
berley 1956, Blum 1968, and Redfield 1972). Here, the
large expanses found along the coasts of the Mid-At-
lantic and New England states are rare.

*Spartina patens* is a slender-culmed grass with nar-
row, 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 sum-
mer, 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 under-
neath 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 sys-
tem where Great Bay Boulevard crosses over Little
Thorofare Creek, Tuckerton, Ocean County, New Jer-
sey, USA. The marsh vegetation was dominated by
the two marsh grasses *Spartina patens* and *S. alter
niflora* 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 m².

**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 sys-
tem 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 en-
nesheed, 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 pro-
file of five zones was determined by carefully sorting
through a 0.3-m² swath of each stratum by hand and
scoring the number of each species. Separate but near-
by 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 con-
stituted 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 lo-
cation 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 distri-
butions 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 spe-
cialized in their exploitation of resources (=relative
niche width) along the three ecotope dimensions was
determined by using the following formula (Levins
1968):

\[ B = \frac{1}{n} \sum \frac{P_i^2}{P_i^2} \]

where \( B \) is relative niche width, \( P_i \) is the proportion
of a species (expressed as a decimal) in the \( i \)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 ex-
ample, a sap-feeder which is equally abundant in all
glass 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:

\[ O_{ij} = 1.0 - 0.5 \sum_{h=1}^{S} \left| P_{ih} - P_{jh} \right| \]

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 equiv-
alent 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 regu-
larly occurred on S. patens. Of these, four were plant-
hoppers (Delphacidae), Delphacodes detecta (Van
Duzee), Neomegamelanus dorsalis (Metcalf), Tumu-
dagina minuta McDermott, and Megamelus lobatus,
Am = Amplicephalus simplex, Ml = Megamelus lobatus, As =
Aphelonema simplex, Nd = Neomegamelanus dorsalis. Data
from Raup and Denno (1979).

![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 = Tumidagaena 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).]

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 up-
right 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 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 (Oij) in the microhabitat distributions of sap-feeders inhabiting the S. patens grass system. Dd = Delphacodes detecta, Nd = Neomegamelanus dorsalis, Ams = Amplicephalus simplex, As = Aphelomema simplex, Tm = Tumidagena minuta, Ml = Megamelus lobatus, and Db = Destria bisignata.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>Ml</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>.914</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ams</td>
<td>.908</td>
<td>.830</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>As</td>
<td>.640</td>
<td>.727</td>
<td>.576</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>.286</td>
<td>.290</td>
<td>.274</td>
<td>.279</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ml</td>
<td>.100</td>
<td>.106</td>
<td>.089</td>
<td>.094</td>
<td></td>
<td>.727</td>
<td>1.000</td>
</tr>
<tr>
<td>Db</td>
<td>.040</td>
<td>.045</td>
<td>.028</td>
<td>.034</td>
<td></td>
<td>.489</td>
<td>.041</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Resource dimension</th>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>Ml</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microhabitat</td>
<td></td>
<td>.632</td>
<td>.640</td>
<td>.596</td>
<td>.436</td>
<td>.493</td>
<td>.261</td>
<td>.359</td>
</tr>
<tr>
<td>Season*</td>
<td></td>
<td>.355 (3)</td>
<td>.409 (3)</td>
<td>.249 (1)</td>
<td>.428 (2)</td>
<td>.409 (2)</td>
<td>.381 (2)</td>
<td>.313 (2)</td>
</tr>
<tr>
<td>Elevation</td>
<td></td>
<td>.757</td>
<td>.224</td>
<td>.720</td>
<td>.679</td>
<td>.482</td>
<td>.766†</td>
<td>.855</td>
</tr>
</tbody>
</table>

**NOTE:** * = Numbers in parentheses indicate the number of generations per year. † = Calculated on D-vac collected insects.

---

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>Ml</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>.875</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ams</td>
<td>.403</td>
<td>.446</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>As</td>
<td>.802</td>
<td>.764</td>
<td>.496</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>.559</td>
<td>.556</td>
<td>.311</td>
<td>.526</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ml</td>
<td>.462</td>
<td>.463</td>
<td>.099</td>
<td>.444</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Db</td>
<td>.602</td>
<td>.506</td>
<td>.142</td>
<td>.611</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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.
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 zMHW 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 (Oij) in the elevational distribution of sap-feeders in *S. patens*.** Species code as in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>Ml</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>.404</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ams</td>
<td>.648</td>
<td>.334</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>As</td>
<td>.647</td>
<td>.124</td>
<td>.586</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>.762</td>
<td>.247</td>
<td>.510</td>
<td>.578</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ml</td>
<td>.561</td>
<td>1.99</td>
<td>.766</td>
<td>.723</td>
<td>.563</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Db</td>
<td>.794</td>
<td>.342</td>
<td>.643</td>
<td>.753</td>
<td>.700</td>
<td>.640</td>
<td>1.000</td>
</tr>
</tbody>
</table>

**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 - Oij) between species pairs along three ecotope dimensions. Species code as in Table 1.

<table>
<thead>
<tr>
<th>Species pairs</th>
<th>Season</th>
<th>Elevation</th>
<th>Microhabitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd-Nd</td>
<td>.12</td>
<td>.60*</td>
<td>.09</td>
</tr>
<tr>
<td>Dd-Tm</td>
<td>.44</td>
<td>.24</td>
<td>.71*</td>
</tr>
<tr>
<td>Dd-MI</td>
<td>.54</td>
<td>.44</td>
<td>.90*</td>
</tr>
<tr>
<td>Dd-Ams</td>
<td>.60*</td>
<td>.35</td>
<td>.09</td>
</tr>
<tr>
<td>Dd-Db</td>
<td>.40</td>
<td>.21</td>
<td>.96*</td>
</tr>
<tr>
<td>Dd-As</td>
<td>.20</td>
<td>.35</td>
<td>.36*</td>
</tr>
<tr>
<td>Nd-Tm</td>
<td>.44</td>
<td>.75*</td>
<td>.71</td>
</tr>
<tr>
<td>Nd-MI</td>
<td>.54</td>
<td>.80</td>
<td>.89*</td>
</tr>
<tr>
<td>Nd-Ams</td>
<td>.55</td>
<td>.67*</td>
<td>.17</td>
</tr>
<tr>
<td>Nd-Db</td>
<td>.49</td>
<td>.66</td>
<td>.96*</td>
</tr>
<tr>
<td>Nd-As</td>
<td>.24</td>
<td>.88*</td>
<td>.27</td>
</tr>
<tr>
<td>Tm-MI</td>
<td>.33</td>
<td>.44*</td>
<td>.27</td>
</tr>
<tr>
<td>Tm-Ams</td>
<td>.69</td>
<td>.49</td>
<td>.73*</td>
</tr>
<tr>
<td>Tm-Db</td>
<td>.27</td>
<td>.30</td>
<td>.51*</td>
</tr>
<tr>
<td>Tm-As</td>
<td>.47</td>
<td>.42</td>
<td>.72*</td>
</tr>
<tr>
<td>Ml-Ams</td>
<td>.90</td>
<td>.23</td>
<td>.91*</td>
</tr>
<tr>
<td>Ml-Db</td>
<td>.32</td>
<td>.36</td>
<td>.60*</td>
</tr>
<tr>
<td>Ml-As</td>
<td>.56</td>
<td>.28</td>
<td>.91*</td>
</tr>
<tr>
<td>Ams-Db</td>
<td>.86</td>
<td>.36</td>
<td>.97*</td>
</tr>
<tr>
<td>Ams-As</td>
<td>.50*</td>
<td>.41</td>
<td>.42</td>
</tr>
<tr>
<td>Db-As</td>
<td>.39</td>
<td>.25</td>
<td>.97*</td>
</tr>
</tbody>
</table>

\[ \bar{x} \pm \sigma = .47 \pm .19, .45 \pm .19, .62 \pm .30 \]

* = 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 - Oij) (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 \( \chi^2 \) 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>MI</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>.033</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ams</td>
<td>.024</td>
<td>.008</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>As</td>
<td>.43</td>
<td>.006</td>
<td>.015</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>1.416</td>
<td>1.395</td>
<td>1.372</td>
<td>1.481</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MI</td>
<td>2.158</td>
<td>2.143</td>
<td>2.082</td>
<td>2.357</td>
<td>.383</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Db</td>
<td>2.186</td>
<td>2.170</td>
<td>2.086</td>
<td>2.499</td>
<td>.127</td>
<td>.415</td>
<td>0</td>
</tr>
</tbody>
</table>

NOTE: 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 $d/l(\sigma^2 + \sigma_z^2)$ 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 ($d/l(\sigma^2 + \sigma_z^2) > 1$ 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 $d/l(\sigma^2 + \sigma_z^2)$ 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 $d/l(\sigma^2 + \sigma_z^2)$ 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 $=1.0$ 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.

![Figure 7](image-url) **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.
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, \( Ams. \) 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 \( Ams. \) 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 \( Ams. \) 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>
<thead>
<tr>
<th>Species</th>
<th>Dd</th>
<th>Nd</th>
<th>Ams</th>
<th>As</th>
<th>Tm</th>
<th>Ml</th>
<th>Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dd</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>1.163</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ams</td>
<td>0.331</td>
<td>1.569</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>As</td>
<td>0.560</td>
<td>1.837</td>
<td>0.224</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tm</td>
<td>0.187</td>
<td>1.434</td>
<td>0.163</td>
<td>0.412</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ml</td>
<td>0.554</td>
<td>1.847</td>
<td>0.228</td>
<td>0.018</td>
<td>0.408</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Db</td>
<td>0.134</td>
<td>1.282</td>
<td>0.181</td>
<td>0.390</td>
<td>0.027</td>
<td>0.390</td>
<td>0</td>
</tr>
</tbody>
</table>
June 1980

ECOTOPE DIFFERENTIATION IN SAP-FEEDERS 711

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 cited herbivorous insects that spend most of their lives on single plant parts as an example. Four species: Delphacodes detecta, Neomegamelanaxis dorsalis, Aphelomema simplex, and Amplicephalus simplex occurred primarily above the thatch layer in the upper stratum of their host grass. Another three species, Tumidagena minuta, Megalmelus lobatus, and Destria bisignata existed within and beneath the thatch in the lower stratum. There was evidence for further microhabitat partitioning 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-

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Dry mass (μ ± σ)</th>
<th>Ratio A</th>
<th>Ratio B</th>
<th>Ratio C</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. dorsalis</td>
<td>.11 ± .008</td>
<td>1.36</td>
<td>.13</td>
<td>1.15</td>
</tr>
<tr>
<td>T. minuta</td>
<td>.15 ± .018</td>
<td>1.67</td>
<td>.12</td>
<td>1.15</td>
</tr>
<tr>
<td>M. lobatus</td>
<td>.25 ± .032</td>
<td>2.73</td>
<td>.20</td>
<td>.15</td>
</tr>
<tr>
<td>D. detecta</td>
<td>.30 ± .037</td>
<td>1.67</td>
<td>1.36</td>
<td></td>
</tr>
<tr>
<td>D. bisignata</td>
<td>.34 ± .012</td>
<td>.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. simplex</td>
<td>.68 ± .036</td>
<td>2.27</td>
<td>.20</td>
<td>.15</td>
</tr>
<tr>
<td>Am. simplex</td>
<td>.78 ± .044</td>
<td>.15</td>
<td>.15</td>
<td></td>
</tr>
</tbody>
</table>

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 > (σ1^2 + σ2^2)) 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.
breads of *D. detecta* and *T. minuta*, the smallest species over most of the elevational range of *S. patens*, are larger than the breadths 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 subguilds (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 macropterus and females brachypterus. 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 (≈1 ha) compared to large (≈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**


