

Comparison of the Assemblages of Sap-Feeding Insects (Homoptera-Hemiptera) Inhabiting Two Structurally Different Salt Marsh Grasses in the Genus *Spartina*¹

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ABSTRACT

The vegetation of New Jersey tidal salt marshes is composed primarily of 2 grasses; *Spartina patens*, which occupies a narrow elevational zone of high marsh and *Spartina alterniflora*, an intertidal species. *S. patens* forms a dense, persistent, thatch, while *S. alterniflora* produces only a loose lattice of litter which rapidly decomposes.

A comparison between the guilds of sap-feeding insects (for the most part, Delphacidae, Cicadellidae, Issidae, and Miridae) inhabiting these grasses reveals *S. patens* housing a much more diverse assemblage of herbivores than *S. alterniflora*. *S. alterniflora*-inhabiting species are exclusively bi- or trivoltine, while on *S. patens*, sap-feeders possess a greater variety of life history types and show a specialized trend toward univoltinism.

Removal of only the dead thatch portion of *S. patens* results in reduced species diversity and evenness of sap-feeders on the living grass system. Trivoltine species, which normally inhabit the upper strata of *S. patens*, increase their populations on detached grass compared to the unaltered grass system.

Both empirical and experimental evidence suggests that the complex microstructure and thatch of *S. patens* provide a more heterogeneous and protective resource which supports a more diverse and specialized fauna of sap-feeders than *S. alterniflora*.

Murdoch et al. (1972) and Allan et al. (1975), respectively, show that the species diversity of Homoptera and arthropods correlates with the foliage height diversity of field vegetation. Also, there is a positive correlation between mean vegetation height and the richness and diversity of Auchenorrhyncha (Homoptera) inhabiting grassland habitats (Morris 1971, 1974). In addition to the inherent structural complexity of the living portion of vegetation, certain plants, particularly some of the grasses, have an associated basal thatch of dead culms and blades (Blum 1968). Grasses which produce a persistent thatch have an added component of structural diversity which thatchless species lack. Such grasses may provide additional oviposition sites, protection from physical stresses, and refuge from predators or parasites, characteristics which might increase the reliability and/or heterogeneity of the resource, leading to an increase in the number of resident herbivores. Furthermore, the presence of a basal thatch may dictate moisture, temperature and light gradients along the vertical axis of the living grass system, further increasing the number of microhabitats, and possibly allowing for the coexistence of additional phytophagous insects. Morris (1975) substantiated this hypothesis in part when he found a more diverse community of Auchenorrhyncha associated with unburned areas of grassland than habitats where litter was removed by burning.

Spartina alterniflora Lois. (Salt Marsh Cordgrass) and *Spartina patens* (Ait.) Muhl. (Salt Meadow Cordgrass) are 2 grasses that dominate the vegeta-

tion of tidal salt marshes along the northeast coast of North America. *S. patens* forms a dense persistent thatch composed of dead plants from 3 or more previous growing seasons, while the dead culms of *S. alterniflora* form a loose lattice that decomposes rapidly over the course of the following year (Blum 1968). To test the prediction that structurally complex, thatch-forming grasses house a more diverse fauna of phytophagous insects than thatch-free grasses, I compared the assemblages of sap-feeding insects residing in *S. patens* and *S. alterniflora*. In order to further investigate this prediction, thatch was removed from small plots of *S. patens* and the responses of herbivorous insects were measured.

Structure of Host Grasses

S. patens (hereafter abbreviated SP) occupies a narrow elevational zone of well-drained high marsh above mean high water level (MHW), where it can grow in extensive pure stands that are occasionally inundated by tides (Redfield 1972). SP is a slender-culmed grass with narrow, convoluted blades (Moberly 1956, Blum 1968). The culms of SP 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 of SP fold over at a weak area in the stem which coincides approximately with that portion of the stem that is included

¹This report is a paper of the Journal Series, New Jersey Agric. Exp. Stn., Rutgers—the State University of New Jersey, New Brunswick, NJ. The study was supported by a grant from the New Jersey State Mosquito Commission.

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in and surrounded by the dead thatch (Blum 1968). Prostration usually occurs in a mosaic fashion, leaving behind small "islands" of somewhat erect plants.

If the structure of SP were examined during summer, one would find 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.

S. alterniflora, an intertidal grass, occurs throughout most of the elevational range of SP, but also extends to levels far below MHW (Adams 1963, Blum 1968, and Redfield 1972). There are 2 distinct growth forms of *S. alterniflora*. Near MHW, where the marsh is flat, *S. alterniflora* grows as a short form (hereafter abbreviated SAS), consisting of stiff rosettes of flat, divergent, leaves, that attain a height of only 1–4 dm. Dead blades and culms of SAS fall in place on the moist marsh to form a loose lattice of litter, which rapidly decomposes over the course of the following year (Burkholder and Bornside 1957, Squiers and Good 1974). Reduced culm density and the lack of extensive thatch allow for exposure of the marsh surface in SAS habitats.

Along the depressed borders of natural tidal creeks, at elevations well below MHW, tall-form *S. alterniflora* (hereafter abbreviated SAT) grows, where the culms commonly reach heights over 2 m. On most New Jersey salt marshes, there are extensive areas of flat high marsh covered by SAS which abruptly intergrade, over the distance of a few meters, into SAT along the depressed margins of creeks.

New shoots of SAS and SP appear in spring, and maximum, above-ground, living, standing crop is attained in July or Aug. on New Jersey marshes (Squiers and Good 1974, Busch 1975). Maximum standing crop values for SAS and SP are similar. Nixon and Oviatt (1973) report 432 and 430 g dry wt/m², respectively, for SAS and SP on a Rhode Island salt marsh; Squiers and Good (1974) obtained a standing crop of 592 g/m² for SAS on a New Jersey marsh; and Busch (1975) also working in New Jersey, recorded peak standing crop values of 402 g/m² and 479 g/m² respectively for SAS and SP.

Study Site and Methods

The study site was an extensive salt marsh in the Barnegat National Wildlife Refuge located approximately 3 km E. of Manahawkin, Ocean Co., NJ (39°, 42' N. Lat., 74°, 15' W. Long.). Both SAS and SP occurred as a mosaic of large (>1 ha), primarily pure stands. By measuring aerial photographs with a planimeter, the relative cover of SAS and SP was calculated at 52% and 48%, respectively. SAT fringed the natural creeks and ditches on the marsh and represented an insignificant percentage of the total grass cover.

A sampling area was established which incorporated a large expanse of both SAS (mean culm

height in Aug. was 32.8 cm) and SP. Using a 38.1 cm diam (=15") standard sweep net, insects were sampled on 28 dates at approximately one wk intervals between March and Dec., 1974. Each sample consisted of 30 sweeps taken while walking through pure stands of each grass. Five samples were taken from each grass habitat on each date. Swept insects were killed in a large ethyl-acetate jar, transferred to 250 ml alcohol (95% ethanol) bottles, and returned to the laboratory, where they were sorted to species and instar, and counted.

The advantages of the sweep net over other sampling methods lies with its ability to collect large numbers of widely dispersed and fast-moving insects (Southwood 1966). A few species were observed to occur primarily beneath the thatch of SP; these sap-feeders were probably slighted by the net. In order to minimize some of the inadequacies of the sweep net as a sampling tool, posed by various authors (DeLong 1932, Gray and Treloar 1933, and Beall 1935), samples were taken on clear (<50% cloud cover), usually warm (>19°C) days, in dry vegetation within 2 h of noon, when most species were observed to move into horizons of vegetation sampled by the net.

To examine the responses of herbivorous insects to thatch removal, 3 separate square plots, each 100 m² and separated from one another by ca. 25 m, were selected in a pure stand of SP. Using electric lawn clippers and large knives, virtually all above-ground vegetation (including thatch) was removed from 2 of the plots during the winter (Jan., 1975) and the unclipped plot was used as a control. Shoots of the perennial grass appeared in both dethatched plots and the control area in spring. To determine the effect of thatch removal on grass growth and to demonstrate the efficiency of dethatching, I sampled both living and dead components of the standing crop biomass of SP during March, mid-June, and again in late July (peak standing crop) in each of the 3 plots. Standing crop was determined by clipping all grass within a randomly tossed 0.047 m² wire quadrat [recommended by Wiegert (1962) as optimum quadrat size for sampling grass vegetation], sorting living plants from dead thatch, drying each component at 100°C for 24 h, and weighing each portion. Five samples were taken from each plot on each date.

Insects were sampled on June 17, July 23, Aug. 20 and Sept. 20 by taking 5 samples (10 sweeps/sample) in the unclipped and dethatched plots on each date. Sweep transects were taken in parallel, nonoverlapping swaths in each plot, while keeping 1 swath-width from the plot edge. Captured insects were processed according to the method outlined above.

The removal of thatch during the winter, leaving little vegetation on the exposed marsh surface, certainly must be viewed as a large scale perturbation. Exploitation of the living grass in the dethatched plots the following season is completely dependent on immigration of insects from adjacent source areas. To ensure that any differential response by the in-

sect community recorded in the clipped areas was due to the absence of thatch and not to retarded rates of recolonization, plots were purposely kept small, and insect sampling was not initiated until 5 mo following the removal of thatch.

Herbivore diversity for each sample was measured using the Shannon-Weaver information index (Shannon 1948):

$$H' = -\sum_{i=1}^s p_i \ln p_i,$$

where H' is the amount of diversity in a group of species, s is the number of species under consideration, p_i is the relative abundance of the i^{th} species, and $\ln p_i$ is the natural logarithm of p_i . The evenness component of species diversity was measured by the ratio of observed diversity to the maximum possible diversity for a particular set of species and individuals (Pielou 1966):

$$J' = H'/H \text{ max.} = H'/\ln S,$$

where J' is evenness, H' is the observed diversity and $\ln S$ ($=H \text{ max.} = \text{maximum diversity}$) is the natural logarithm of the number of species in the set. Species diversity (H') has no theoretical upper bound and is limited only by a finite number of species. Species evenness, on the other hand, is constrained between 0 and 1.0.

In order to measure the relative success of a phytophagous species in dethatched grass compared to grass having thatch, I used the following index:

$$SI = N_{t+1}/A_t,$$

where SI is the index of success, N_{t+1} is the density of nymphs at time $t+1$ and A_t is the density of adults at time t . A number of factors associated with the quality of oviposition sites and the suitability and harshness of nymphal habitats could lead to small densities of nymphs at time $t+1$ relative to adult densities at time t , reducing the success of the species, and documenting the inferior nature of a particular habitat for insect development. The validity of the index is dependent upon the assumption that the number of adults present at time t is representative of those adults which potentially could contribute to the density of nymphs at time $t+1$. To best meet this assumption, the time interval $t+1-t$ should approach the generation time of the species so that the nymphs measured are indeed the offspring, and not the contemporaries, of the adults. Because of irregularities in the sampling interval $t+1-t$, the absolute value of the success index (SI) is trivial, but the magnitudes of indices can be used to compare the relative success of a species under 2 or more different conditions as long as the same time interval is used and the generations of the species developing under both conditions are relatively synchronous.

Results

Comparison of Sap-feeder Richness and Diversity Between Grass Associations

The number of resident species, species diversity,

and the evenness component of species diversity of sap-feeders were measured throughout most of the year in SP and SAS (Fig. 1). Except for the winter and early spring months, the number of resident species was significantly higher in SP than SAS ($F_{1,224} = 1454.38$; $P << .001$). In both grasses, the only species taken during the winter season were delphacids, which overwintered as nymphs. With the onset of spring, overwintering eggs of Cicadellidae, Issidae, and Miridae hatched and accounted for most of the increase in species richness. The richness of sap-feeders in SP increased rapidly in May and reached a peak during early July, after which there was a steady decline until winter when minimum values were recorded. In SAS, the seasonal trend of species richness was similar, but maximum values were obtained during the fall.

Sap-feeder diversity (H') was also significantly higher in SP compared to SAS on most sample dates ($F_{1,224} = 1956.98$; $P << .001$). There was a conspicuous peak of sap-feeder diversity during May in SP, but values oscillated around 0.7 for the remainder of the year. Contrary to the pattern of sap-feeder diversity in SP, diversity was highest during winter and early spring in SAS. Throughout most of spring and summer, near 0.0 values of sap-feeder diversity were obtained in SAS. Dense populations of the delphacid, *Prokelisia marginata* (Van Duzee), were primarily responsible for the low species diversity in SAS.

The evenness of sap-feeding species (J') was highest during the spring and winter seasons in both salt marsh grasses. Species evenness was consistently low during spring and summer in SAS, and in summer and early fall in SP. Generally, evenness was significantly higher in SP compared to SAS ($F_{1,224} = 562.59$; $P << .001$).

I examined the relationships of the richness, diversity, and evenness of sap-feeders with the seasonal growth pattern of each respective host grass. This was accomplished by correlating sap-feeder richness, H' , and J' with corresponding seasonal values of living, above-ground, standing crop biomass of both grasses. Standing crop values for SP and SAS were taken from Busch (1975), who sampled the same marsh during the same year as I did.

The correlation between sap-feeder richness and grass standing crop was significant in both SP ($y=3.409 + 0.209x$, $n=28$, $r=.816$, $P < .01$) and SAS ($y=1.938 + 0.096x$, $n=28$, $r=.531$, $P < .01$) (Fig. 2). The same correlation using sap-feeder diversity (H') was not significant with either SP ($y=0.650 + 0.002x$, $n=28$, $r=0.67$, $P > .05$) or SAS ($y=0.169 - 0.009x$, $n=28$, $r=-.356$, $P > .05$). Evenness was negatively correlated with grass standing crop in SP ($y=0.591 - 0.014x$, $n=28$, $r=-.578$, $P < .01$) and SAS ($y=0.220 - 0.020x$, $n=28$, $r=-.450$, $P < .05$) (Fig. 3).

The structure of each respective guild of sap-feeders exploiting SP and SAS is summarized in Fig. 4, where species are ranked according to their

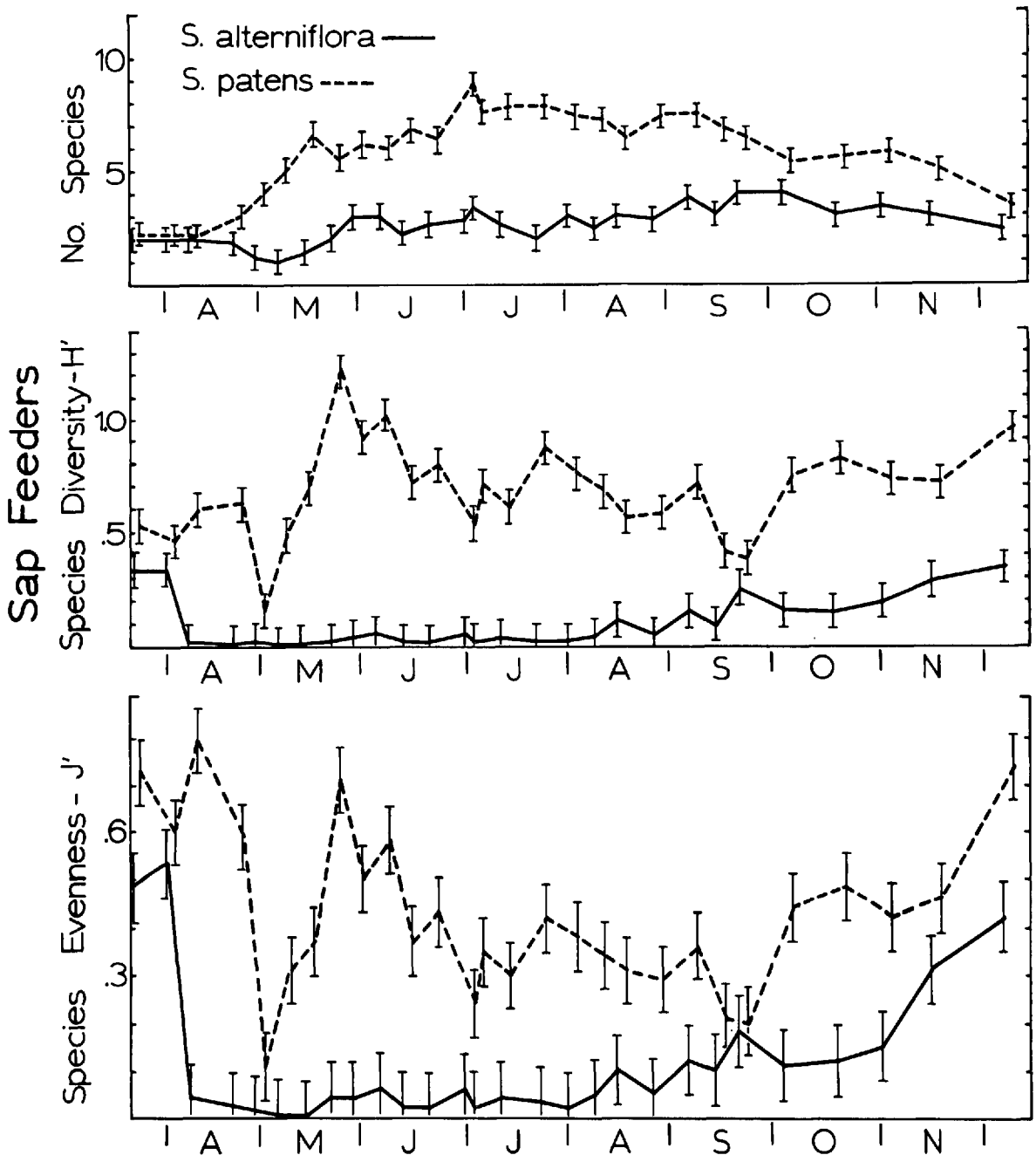


FIG. 1.—Seasonal patterns of sap-feeder richness, diversity (H'), and evenness (J') in the salt marsh grasses, *Spartina alterniflora* and *S. patens*. Statistical intervals surrounding means are Least Significant Intervals (LSI). Graphical nonoverlap of intervals connotes significance among means at the 5% probability level.

abundance in each habitat. Eleven residents, that developed at least one generation of adults per year, (4 Delphacidae, 4 Cicadellidae, 1 Issidae, 1 Eriococcidae, and 1 Pentatomidae) were sampled in SP. Only 5 sap-feeders (3 Delphacidae, 1 Cicadellidae, and 1 Miridae) were sampled on SAS. The dominant herbivores in both grasses were delphacids, *Delphacodes detecta* (Van Duzee) in SP and *Prokelisia marginata* (Van Duzee) in SAS. The SP association also supported a series of subdominants, *Tumidagena*

minuta McDermott (Delphacidae), *Eriococcus n. sp.* (Eriococcidae), *Aphelonema simplex* (Uhler) (Issidae), and *Amplicephalus simplex* (Van Duzee) (Cicadellidae), which were not as abundant as *D. detecta*, but had a seasonal total of individuals > 1000. The lack of subdominant residents in a community completely dominated by *P. marginata* was primarily responsible for the low species diversity and equitability of the sap-feeding guild in SAS compared to SP.

Assemblage of Sap-feeders Inhabiting Spartina patens

The seasonal density patterns of nymphs and adults of each species were monitored. Particular attention was paid to the number of generations that developed each year, the proportion of the year during which active stages occurred, and the overwintering stage and its location in the grass.

The seasonal abundance of the nymphs and adults of the planthopper, *D. detecta*, is pictured in Fig. 5. Overwintering took place primarily as 4th or 5th instars. The occurrence of 1st instars only after the appearance of adults in spring is strong evidence that eggs are not present on the marsh during the winter months. Peaks of adult density occurred during May, early July and late Aug. for this trivoltine planthopper. The largest population of adults was achieved in July during the 2nd generation, although adult levels remained high until mid-Sept. Nymphal populations increased throughout the growing season of the grass, peaking in late Sept. Active instars were sampled year-round.

Nymphs and adults of *D. detecta* were observed to inhabit primarily the upper strata of the grass system consisting of seed heads and both erect and matted culms and blades above the horizon of dead

thatch. During cold weather active stages descended into the thatch.

Neomegamelanus dorsalis (Metcalf) (Delphacidae), has a life history similar to *D. detecta*, but was a very uncommon species (Fig. 5). Overwintering nymphs matured to a small population of adults during late May. Two larger peaks of adult density occurred during July and Sept. Active stages were taken during every month of the year. *N. dorsalis* also occurred primarily in the upper strata of the grass and active stages were seldom observed within or beneath the thatch horizon.

Tumidagena minuta McDermott passed the winter as 4th instars in the thatch of SP. Although active stages were collected all year, this planthopper was bivoltine, with peaks of adult abundance occurring in late May and again during late July (Fig. 5). Nymphal populations increased throughout the season, attaining a maximum in late Oct. The generations of *T. minuta* were far more discrete than those of *D. detecta*, probably due to a more synchronized pattern of oviposition during the earlier part of the season.

Although nymphs and adults of *T. minuta* occurred on the upper parts of the grass, they were also observed within the thatch and beneath the thatch

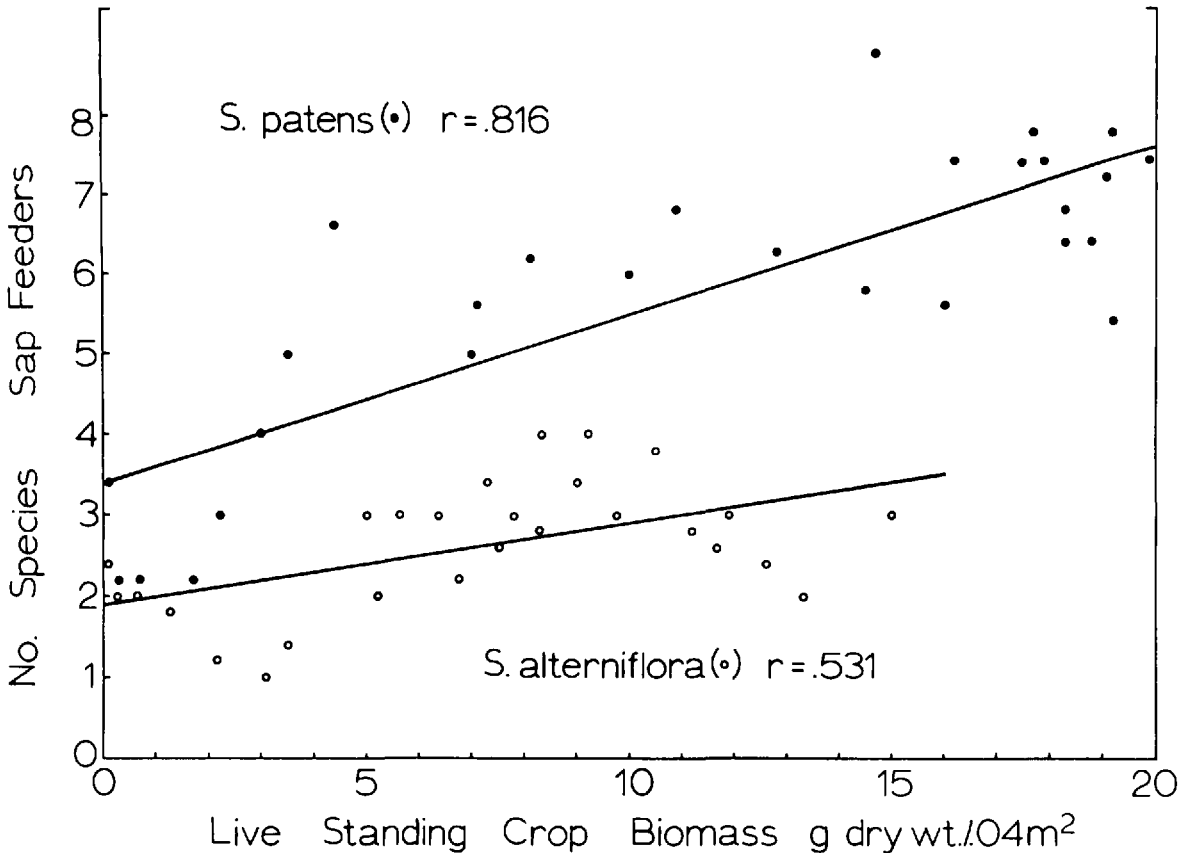


FIG. 2.—Relationship between sap-feeder richness and the live standing crop biomass (g dry wt./0.04m² of *Spartina alterniflora* and *S. patens*).

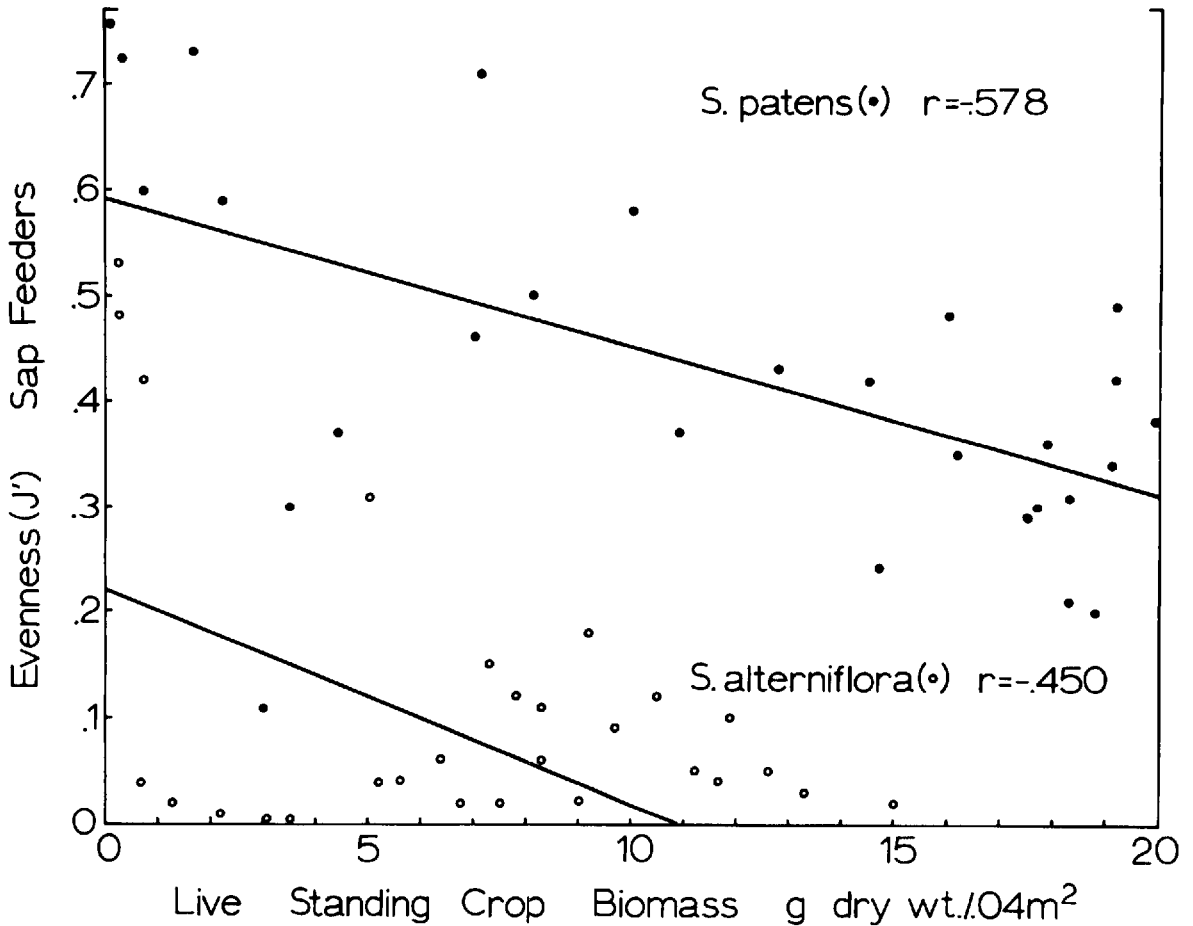


FIG. 3.—Relationship between the evenness (J') of sap-feeding species and the live standing crop biomass (g dry wt./0.04m²) of *Spartina alterniflora* and *S. patens*.

associated with the new tillers sprouting from the crown. Because of this distribution, the relative population of *T. minuta* was probably underestimated.

A 4th delphacid, *Megamelus lobatus* Beamer, also occurred in SP. Unlike the planthoppers already discussed, field observations documented that *M. lobatus* remained beneath the surface of the thatch for most of its life history, surfacing only occasionally, which explained its sporadic and rare appearance in samples. The largest number of adults was taken during late Oct. and Nov., but 2 other small peaks of adults appeared during early July and late Aug. Except for the fall generation, adult occurrence was followed by the patchy appearance of nymphs. The absence of nymphs during the winter season and the appearance of 1st instars during late spring suggests that while *M. lobatus* is trivoltine, it differs in its life history from the other delphacids because eggs are the overwintering stage.

Density trends for the nymphs and adults of *Aphelonema simplex* (Uhler) (Issidae) are pictured in Fig. 5. Winter was passed as eggs deposited in the grass culms; these hatched and nymphs first ap-

peared in May. *A. simplex* was bivoltine, with peaks of adult density occurring in late June and Sept. Active stages were absent during the winter and early spring months.

Four leafhoppers, *Destria bisignata* (Sanders and DeLong), *Amplipcephalus simplex* (Van Duzee), *Hecalus lineatus* (Uhler), and *Paraphlepsius sp.* developed on SP. All 4 species overwintered as eggs deposited in grass culms or blades. The seasonal patterns of abundance for the nymphs and adults of 3 of these leafhoppers are shown in Fig. 6. *D. bisignata* was a rare bivoltine species with adults most common during early Sept. and Nov. Both adults and nymphs were collected as late in the season as Dec. *Am. simplex* was the most abundant of the 3 leafhopper species. A single generation of nymphs first appeared in May and adults were most abundant during early July. Seasonal displacement between *Am. simplex* and *D. bisignata* was evident. Nymphs of the rare *H. lineatus* were most abundant during June and one generation of adults appeared in the summer months. Active stages of *Am. simplex* and *H. lineatus* were absent during fall, winter and early spring. *Paraphlepsius sp.* was the rarest of the

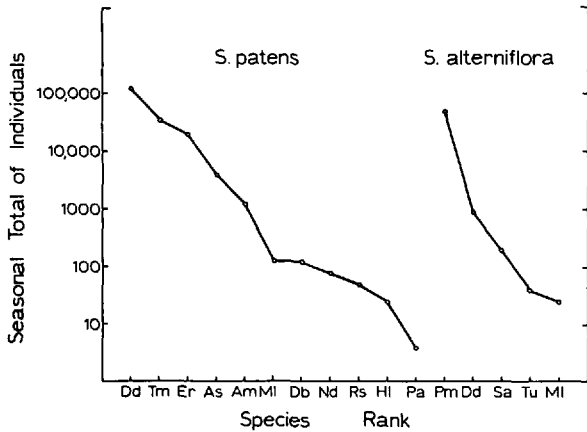


FIG. 4.—Annual total of individuals for each sap-feeding species (pooled weekly means), ranked in order of descending importance in each grass type. Dd=*Delphacodes detecta*, Tm=*Tumidagena minuta*, Er=*Eriococcus n. sp.*, As=*Aphelonema simplex*, Am=*Amplicephalus simplex*, Ml=*Megamelus lobatus*, Db=*Destria bisignata*, Nd=*Neomegamelanus dorsalis*, Rs=*Rhytidolomia saucia*, Hl=*Hecalus lineatus*, Pa=*Paraphlepsius sp.*, Pm=*Prokelisia marginata*, Sa=*Sanctanus aestuarium*, Tu=*Trigonotylus uhleri*.

leafhoppers, but a very few nymphs and adults of this univoltine species were swept during June and July.

A number of species of Homoptera—Sternorrhyncha were collected on SP, but most, because of either their sessile or cryptic habits, were not amenable to sweep net sampling. Only *Eriococcus n. sp.* was captured. Small numbers of both adult males and females appeared during May, followed in early June by a large flux of crawlers that developed into 2nd instars by July (Fig. 6). After July, the population of nymphs in samples decreased rapidly,

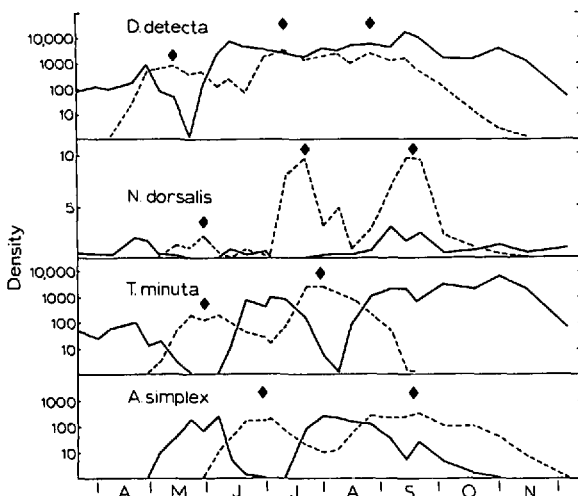


FIG. 5.—Seasonal distribution of the densities of nymphs (solid lines) and adults (dashed lines) of 4 sap-feeders inhabiting *Spartina patens*. Diamonds indicate adult generation peaks.

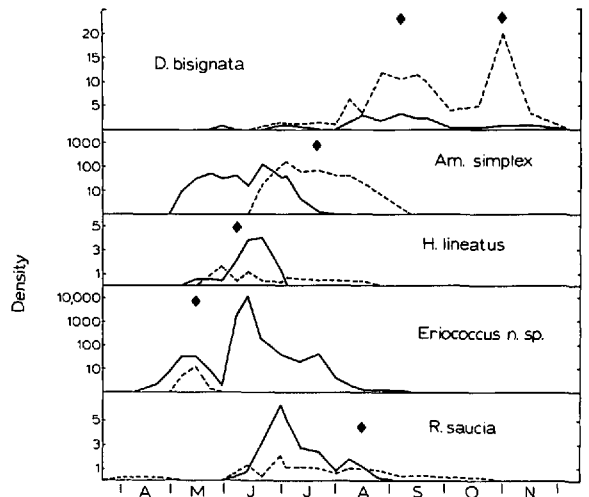


FIG. 6.—Seasonal distribution of the densities of nymphs (solid lines) and adults (dashed lines) of 5 sap-feeders inhabiting *Spartina patens*. Diamonds indicate adult generation peaks.

due probably to a combination of dispersal, mortality, and settling deep into the grass where they overwintered. Apparently, larger nymphs become active again in April when they move to the new grass shoots to complete development. At this time they are again retrieved in samples as evidenced by a spring peak of nymphs prior to the appearance of adults.

Two other coccoids inhabited SP, but were not captured in samples. *Odonaspis sp. nr. litoralis* Ferris (Diaspididae) was quite common under the leaf-sheaths near the crown of the grass. *Saccharicoccus n. sp.* (Pseudococcidae) was uncommon, but small, patchy, populations were encountered in the inflorescences of SP during fall. There are undoubtedly other coccoids which occur on the salt marsh grasses.

One last member of the sap-feeding guild was a large stink bug, *Rhytidolomia saucia* (Say). There was one summer generation of nymphs which reached a peak during the end of June (Fig. 6). Nymphs were preceded in spring and followed in fall by small numbers of adults, suggesting that *R. saucia* overwinters during the adult stage, probably within the thatch of SP.

The species of sap-feeders exploiting SP can be divided into several different life history categories. There are "perpetual species" that are present on the salt marsh as active nymphs or adults throughout the year. All delphacids except *M. lobatus* are "perpetual species," and are either trivoltine (*D. detecta*, and *N. dorsalis*) or bivoltine (*T. minuta*). *Eriococcus n. sp.* and *R. saucia* develop a single generation during the year and overwinter as nymphs and adults, respectively.

In addition to "perpetual species," there are also "seasonal species" that are active on the marsh for only a portion of the year. "Seasonal species" in

SP are trivoltine (*M. lobatus*), bivoltine (*A. simplex* and *D. bisignata*), and univoltine (*Am. simplex*, *H. lineatus*, and *Paraphlepsius* sp.), and undergo an extensive period of inactivity as eggs during winter.

Assemblage of Sap-feeders Inhabiting Short-form *Spartina alterniflora*

The seasonal fluctuations in the densities of nymphs and adults of *P. marginata*, the dominant herbivore, are shown in Fig. 7. Winter was passed primarily as 3rd or 4th instars beneath the loose lattice of dead culms, in rolled dead leaf-blades, or in sheltered blade axils of the dead rosettes. Fifth instars began molting to adults in early April, and the 1st generation of adults reached maximum density in mid-May. July and Sept. peaks of adult abundance marked the 2nd and 3rd generations. Nymphs were present in SAS during every month of the year.

M. lobatus occurred uncommonly in SAS as well as SP. However, the external appearance of the SP- and SAS- entities differed in some respect. Individuals taken from SP were consistently smaller and lighter in color than those residing in SAS. The life history of *M. lobatus* in SAS was, however, similar to that in SP. There were multiple generations, probably 3, with adults and nymphs most abundant during Sept. and Oct., and overwintering took place as eggs.

D. detecta, which was the dominant species in SP, also occurred on SAS (Fig. 7). Macropterous adults (most salt marsh delphacids exhibit wing-polymorphism, see Denno 1976), appeared in SAS habitats during mid-Sept., and a small population of nymphs followed in Oct. By the following April, nymphs were absent in most samples. In May, at which time the spring generation of adults peaked in SP, residual numbers of predominantly macropterous adults occurred in SAS. *D. detecta* was absent from most summer samples. The near absence of adults in

spring suggests that the generation of *D. detecta* may be abortive and that SAS may be an inferior host plant for development. The occurrence of *D. detecta* on SAS during the cold months was the primary factor responsible for the winter increase in species diversity.

One leafhopper, *Sanctanus aestuarium* (DeLong and Slesman), occurred at low densities in SAS (Fig. 7). Two generations of adults were produced, one in June and a 2nd during Sept. The winter was passed as eggs, probably deposited in the dead culms of SAS.

The cryptic green mirid, *Trigonotylus uhleri* (Reuter), was also bivoltine and overwintered as eggs deposited in the vegetation. First instars appeared in May and 1st-generation adults were most abundant during June (Fig. 7). A 2nd peak of adult abundance was evident in Aug. and Sept.

Two coccoids occurred very infrequently on SAS, but were not taken in samples. *Haliaspis spartinae* (Comstock) inhabited the adaxial surface of the leaf-blades of primarily SAT, but was never observed in the study area. An unusual, undescribed genus of Pseudococcidae was found between the leaf-sheath and culm at the crown of SAS plants. The distribution of these 2 coccoids was patchy and individuals could be located only after an extensive search.

The diversity of life history strategies possessed by the sap-feeders inhabiting SP, is lacking in SAS. *P. marginata*, like most of the delphacids in SP, was a trivoltine "perpetual species," which overwintered as nymphs. *M. lobatus* was trivoltine, *S. aestuarium* and *T. uhleri* were bivoltine and all passed the winter as eggs. Although both "perpetual" and "seasonal species" occurred in SAS, there was a notable absence of univoltine sap-feeders.

Effect of Thatch Removal on the Herbivore Fauna of *Spartina patens*

Seasonal changes in the amount of thatch and standing crop of living grass were measured in the unclipped control and dethatched plots (Fig. 8). From March–July there was a gradual decrease in the biomass of dead thatch on the unclipped plot. Very little thatch remained after clipping on either experimental plot and, as the season progressed, there was no evidence that plant debris was transported onto the dethatched plots by tides or winds.

Green shoots had not yet appeared in any of the plots by March. By June, considerable growth had occurred, but the biomass of living vegetation was significantly larger in the unclipped plot compared to the thatch-free areas. During July, when maximum live standing crop occurs for SP, the live biomass sampled on one of the clipped plots was not significantly different from that found on the unclipped plot. However, the avg live standing crop of grass on the 2nd thatch-free plot was lower than that recorded for the other 2 plots. This was not a generalized vegetational response, but was attributable to a low area in the center of the plot where grass growth was thin and patchy, resulting in a

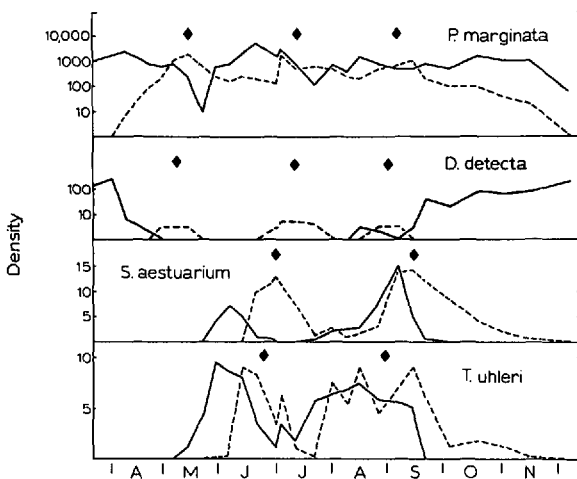


FIG. 7.—Seasonal distribution of the densities of nymphs (solid lines) and adults (dashed lines) of 4 sap-feeders inhabiting *Spartina alterniflora*. Diamonds indicate adult generation peaks.

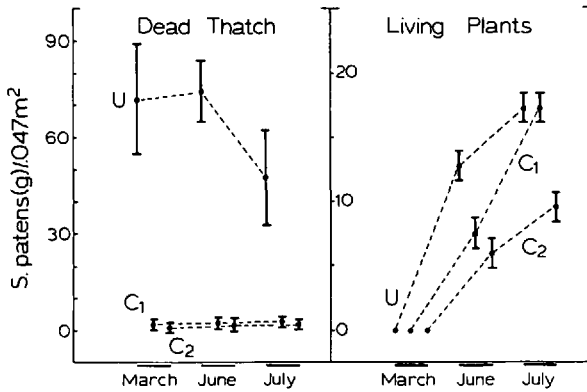


FIG. 8.—Live and dead standing crop biomass of *Spartina patens* (g dry wt./0.047m²) sampled during March, June, and July in both dethatched plots (C₁ and C₂) and the unclipped plot with thatch (U). One standard error surrounds the means for dead standing crop. LSIs for living grass as in Fig. 1.

reduced avg standing crop figure during July. The patchiness of grass standing crop in this clipped plot was evidenced by a coefficient of variation of 54.5%, compared to 33.2% and 29.6% calculated for the other dethatched plot and unclipped plot, respectively. When sweep-netting insects, this thin area was avoided whenever possible.

On each of the 4 sampling dates, the species diversity (H') of sap-feeding insects was significantly lower in plots where the thatch was removed ($F_{2, 48} = 127.76; P << .001$) (Fig. 9). Depressed

values of species diversity in the clipped plots were primarily due to decreases in species evenness (J') (Fig. 9). Both species diversity and evenness declined throughout the season, when in Sept. values near 0.0 were attained.

D. detecta had significantly higher densities of 2nd-generation nymphs during July and 3rd-generation adults in Aug. on both dethatched grass plots compared to the unclipped area (Fig. 10). There were no consistent differences in the densities of either adults or nymphs of *D. detecta* among the plots on any of the remaining sampling periods. Similarly, *N. dorsalis* produced larger populations of 2nd-generation nymphs in Aug. and 2nd-, and 3rd-generation adults during July and Sept. on the dethatched grass plots (Fig. 10).

While some of the sap-feeders increased their populations during at least part of the year on dethatched grass, other species were adversely affected. Populations of 1st-, and 2nd-generation adults of *T. minuta* during June and July, respectively, and 1st-, and 2nd-generation nymphs during July and Sept., respectively, were significantly smaller on dethatched grass than on grass with thatch (Fig. 11).

Very few nymphs or adults of *A. simplex* were ever swept in either dethatched plot during the sample periods (Fig. 11). *A. simplex* overwinters as eggs in the dead grass culms, and it was not surprising to find low densities of 1st-generation nymphs and adults during June in the clipped areas, but this condition also prevailed through the 2nd generation (July and Aug.), implying that adults avoided the colonization of dethatched areas entirely.

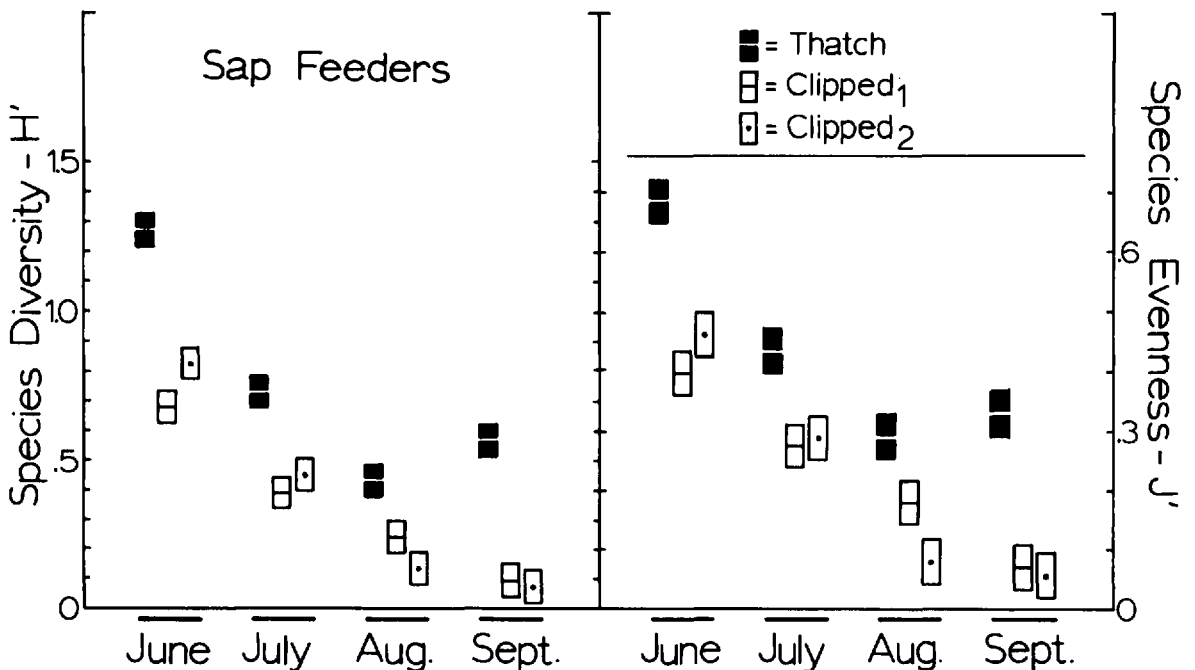


FIG. 9.—Species diversity (H') and evenness (J') of sap-feeding species measured during June, July, Aug., and Sept. in the control plot with thatch and both dethatched plots. LSIs as in Fig. 1.

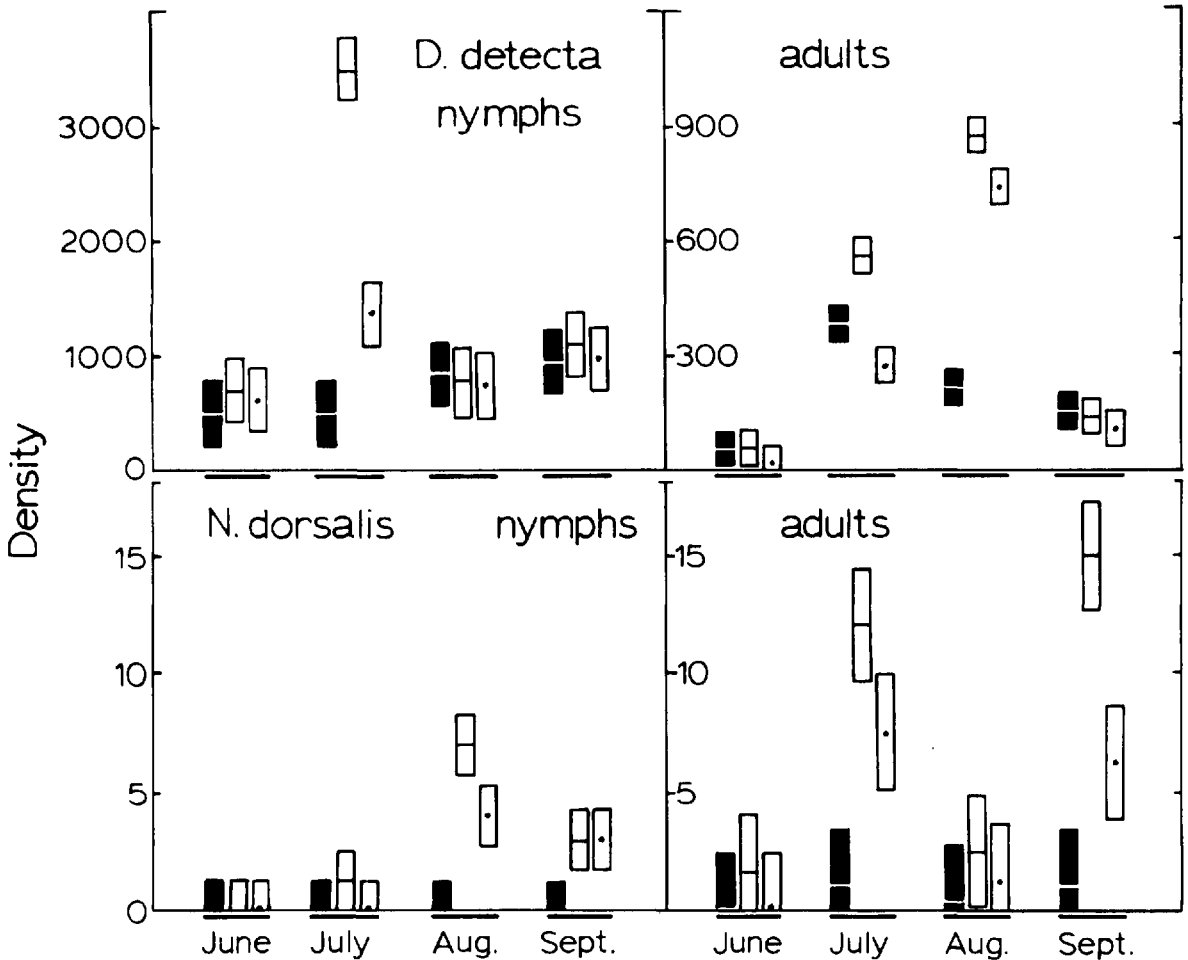


FIG. 10.—Densities of the nymphs and adults of *Delphacodes detecta* and *Neomegamelanus dorsalis* measured during June, July, Aug., and Sept. in the control plot with thatch and both dethatched plots. LSIs as in Fig. 1. Plot legend as in Fig. 9.

The cicadellid, *Am. simplex*, also overwintered as eggs in the dead grass culms, which were removed with dethatching, resulting in significantly smaller populations of 1st-generation nymphs during June in the thatchless grass plots compared to the unclipped area (Fig. 11). However, during July and Aug., there were no significant differences in the density of adults among the plots, suggesting that adults freely recolonized the clipped area.

The relatively low sap-feeder diversity and evenness values recorded on dethatched grass were due to increases in the population size of *D. detecta* and/or reduced densities of *T. minuta*, *A. simplex* and *Am. simplex*.

Indices of success (SI) were calculated at 3 and 2 time periods respectively for populations of *D. detecta* and *T. minuta* occurring on both dethatched grass plots and the unclipped control (Fig. 12). The offspring of 1st-generation adults of *D. detecta* were more successful on dethatched grass compared to SP having a thatch. However, there was no significant difference among the plots in the success of the

nymphs produced by 2nd-generation adults. By the end of the season, either the number of offspring produced by 3rd-generation adults or the number of offspring surviving was significantly lower on grass without a thatch. The success of the offspring of both 1st-, and 2nd-generation adults of *T. minuta* was significantly poorer in dethatched grass than grass with thatch. It is unlikely that reduced nymph density on dethatched grass was the result of emigration because delphacid nymphs, especially early instars, are extremely sessile (Lindsten 1961, Raatikainen 1967).

Predators and Parasites

In order to dismiss the possibility that predation was more severe on dethatched grass than grass with thatch, resulting in smaller populations of *T. minuta* and *A. simplex*, I examined the densities of predators and parasites swept from all plots. Wolf spiders (Lycosidae) were by far the most abundant predators collected in SP. Mirid bugs in the genus *Tythus*, known egg predators of Homoptera, also occurred

sporadically in samples. An analysis of variance performed on the pooled densities of these predators found no significant differences among the 3 plots ($F_{2, 48} = 3.02, P > .05$). Had there been a main plot effect, it is unlikely that a general feeding predator, like a lycosid spider, could account for the selective demise of the populations of *T. minuta* and *A. simplex* on dethatched SP, while the population size of *D. detecta* remained large (Aug. and Sept. of Fig. 10 and 11).

Chrysophagous nr. *americanus* (Perkins), an encyrtid wasp which develops on Cicadellidae, 2 mymarid wasps, *Polynema* sp. and *Gonatocerus* sp., parasites of the eggs of Homoptera, and a dryinid

in the genus *Pseudogonatopus*, which develops primarily on the nymphs of delphacids, were occasionally swept from SP. Fluxes in the population density of a particular parasite, which is presumably specialized in its feeding habit, could account for the reduced population levels of Homoptera recorded on the dethatched grass. However, all of the above parasites were uncommon (<5 individuals/sample) and there were no apparent differences in the densities of these insects between dethatched and unclipped plots. Therefore, it is unlikely that the differences in the responses of the various homopterans to dethatching are attributable to either predation or parasitism.

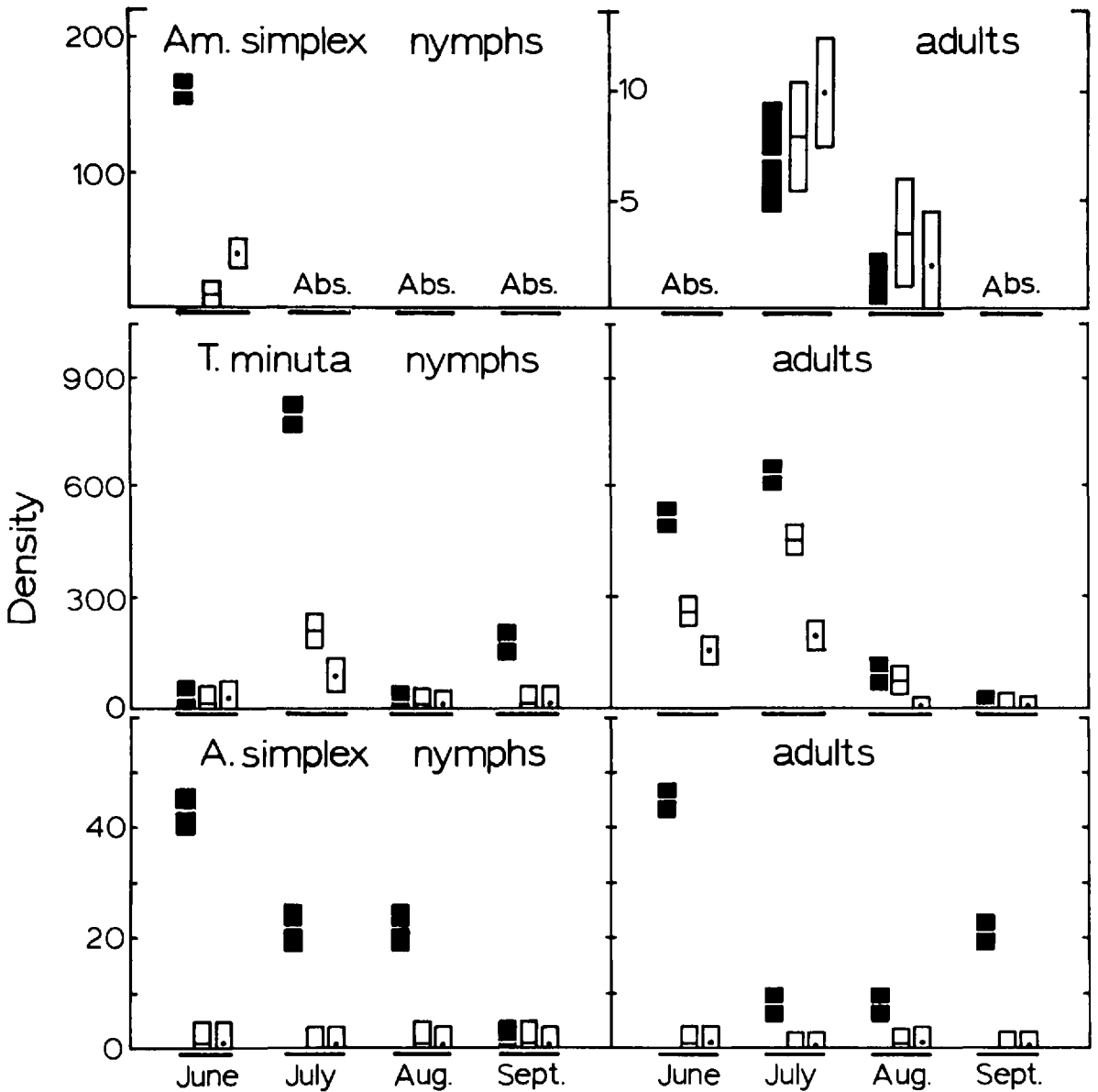


FIG. 11.—Densities of the nymphs and adults of *Amplipcephalus simplex*, *Tumidagena minuta*, and *Aphelonema simplex* measured during June, July, Aug., and Sept. in the control plot with thatch and both dethatched plots. LSIs as in Fig. 1. Plot legend as in Fig. 9. Abs.=Absent.

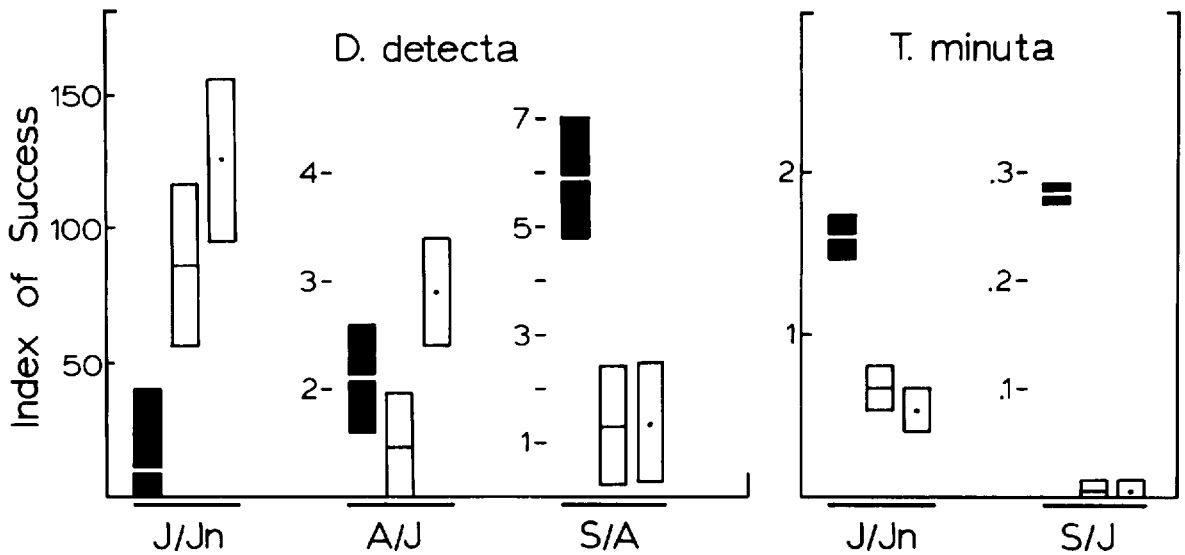


FIG. 12.—Indices of success calculated at 3 and 2 time intervals, respectively, for *Delphacodes detecta* and *Tumidagena minuta* in the control plot with thatch and both dethatched plots. LSIs as in Fig. 1. Plot legend as in Fig. 9. Jn=June, J=July, A=Aug. S=Sept.

Discussion

The data show that SP houses a much more complex community of sap-feeding insects than does SAS. The species richness, diversity (H'), and evenness (J') are higher, and there is a larger variety of life history strategies possessed by the sap-feeders on SP. An obvious trend toward the reduction of the number of generations produced each year by some of the sap-feeders is evident in SP that is not characteristic of SAS-inhabiting species. Univoltine leafhoppers (*Am. simplex*, *H. lineatus*, and *Paraphlepsius* sp.) and Hemiptera (*R. saucia*) occur only on SP, while their counterparts on SAS (*S. aestuarium* and *T. uhleri*) are bivoltine. Only trivoltine fulgoroids occur on SAS, while the fulgoroid fauna of SP consists of both bi- and trivoltine species. The dominant herbivore in both grasses is a "perpetual," trivoltine delphacid; *D. detecta* in SP and *P. marginata* in SAS.

Various hypotheses have been suggested to explain discrepancies in the richness or diversity of the insect community on different plant species. Plants with certain physical or biochemical characteristics are known to prevent or dissuade feeding by many insects and subsequently house a very specialized community of herbivorous insects (Tanton 1962, Agarwal 1964, Pathak 1969, Feeny 1970, 1975, Caswell et al. 1973, Southwood 1973, Root 1975). However, from what evidence exists, there are no blatant differences in the nutritional quality, scheme of carbon-fixation, or leaf microstructure between SP and SAS that would explain the discrepancies in the guilds of sap-feeders on these two grasses (Caswell et al. 1973, Anderson 1974, de la Cruz and Poe 1975).

Two alternatives seem possible when attempting to

explain the differences in sap-feeder diversity between SP and SAS habitats. First, few species may be able to adapt to habitats that are rigorous and continuously subjected to stress (Sanders 1968, MacArthur 1972). However, the elevational difference between the sites occupied by SP and SAS is slight, and although SAS incurs flooding at a greater frequency and for a longer duration, neither habitat is completely inundated except by high spring or storm tides. Cameron (1976), taking samples during and after flooding, showed that periodic tidal inundation had little effect on the number of species or the structure of the insect community in general. Nevertheless, it is not the normal regime of tides which seems potentially destructive to the insect inhabitants, but the intense pounding action of storm tides and waves, and it is likely that in SAS habitats where plant distribution is diffuse and thatch is scanty that insect mortality during such catastrophies is high. The dense thatch found in SP may buffer the action of storms and confer greater reliability to the resource, allowing for the coexistence of more sap-feeding species. Davis and Gray (1966) reasoned similarly when they concluded that *Distichlis* (a salt marsh grass similar in structure to SP) sustains a larger insect fauna than SA because it provides for greater protection from physical factors.

MacArthur (1972) has suggested that there are more species where the environment is complex and therefore more readily subdivided. SP, with its dense entanglement of living and dead plant parts, certainly provides a greater diversity of microhabitats, which could be of potential use to sap-feeders for feeding, oviposition, and hiding. As grass biomass increases to a maximum during the summer, there is a commensurate increase in structural diversity (Blum 1968). This is especially true in SP after leaf-blade

and culm prostration takes place. As plant structural diversity increases, the coexistence of additional sap-feeder species, which specialize on the various plant-parts, is allowed, probably explaining the positive correlation between herbivore richness and grass biomass. Cameron (1972) also surmised that the summer increase in the vegetational diversity of *Spartina foliosa* Trin. was primarily responsible for the packing of additional species of phytophagous insects onto this Pacific Coast salt marsh grass.

When the structural complexity of SP was reduced by removing thatch, the diversity of sap-feeders decreased. This was primarily due to increases in the populations of *D. detecta* and/or population decreases of *T. minuta*, *A. simplex* and *Am. simplex*. Following winter dethatching, spring nymphal populations of *A. simplex* and *Am. simplex* were small, suggesting that the persistent mat of dead SP culms provides a reliable overwintering site for eggs and encourages the residence of "seasonal species." SAS, which forms only a loose, lattice-work of dead culms, houses fewer "seasonal species," none of which becomes very abundant (e.g., *S. aestuarium* and *T. uhleri*).

Indices of success were significantly lower for *T. minuta* on dethatched grass compared to SP with thatch, indicating either the relative failure of both 1st-, and 2nd-generation adults to find suitable oviposition sites or the reduced survival of their eggs or nymphs. *D. detecta* showed a somewhat different response to dethatching. Proportionately larger numbers of offspring were either left by 1st-generation adults or survived on dethatched SP during early summer, but by fall, this pattern changed and the offspring of 3rd-generation adults were proportionately more successful on grass with thatch. The reduced success of *D. detecta* on dethatched grass is probably attributable to characteristics of the senescing host-plant or physical mortality factors which take a greater toll on the nymphs at the end of the season on the exposed grass. The lack of consistent differences in the densities of predators, especially spiders, between dethatched and natural grass suggests that predation is probably not responsible for the reduced success of *D. detecta* on dethatched grass during fall.

When SP is dethatched, the portion of the living grass system once contained within and beneath the thatch becomes readily accessible and it is not surprising to find population increases in those species (*D. detecta* and *N. dorsalis*) which occupy the upper plant strata. Likewise, dethatching destroys those microhabitats contained in and below the thatch, and subsequently, populations of *T. minuta* which partially reside in the thatch horizon were reduced.

"Perpetual species," which are present as active forms year-round, must necessarily be adapted to a broad set of changing biotic and physical conditions when occurring in a temperate region. Advantages to producing multiple generations each year and being "perpetual" lie with the potential for high rates of population increase. By overwintering as a

nymph, resource utilization can begin as soon as suitable conditions for development occur. Compared to "perpetual species," "seasonal species" which occur actively for only a few months during the year (e.g., the univoltine homopterans *Am. simplex* and *H. lineatus*) are relatively specialized in their use of resources along a seasonal time continuum, and relinquish, in part, the potential for high rates of population increase.

The particular strategy of a species is ultimately determined by the reliability of its resources (Southwood et al. 1974). Where host-plant resources are unreliable, that is small, poor in quality, ephemeral, or occur in rigorous habitats, a generalized strategy on the part of exploiting insects is usually favored. As the reliability of the resource base increases, selection should favor the efficient use of that resource with the development of a specialized utilization strategy (Pianka 1970, Southwood et al. 1974).

If SP is more reliable than SAS, one might expect to find more specialized sap-feeders there. Even though both grasses were dominated by "perpetual species," with apparently high reproductive capacities, univoltine seasonal specialists occurred only in SP. There was a common tendency for these univoltine species to develop as nymphs during May and June. This is probably the result of selection pressures which synchronize feeding and development with optimum resource conditions. Optimum conditions for SP occur during May and June when the grass is nearing maximum productivity and still very fresh, not having deteriorated due to natural senescence or feeding and oviposition by the bi- or trivoltine species which reach maximum population densities later in the season.

When the natural structure of the SP habitat was altered by removing thatch, population increases were observed only for the trivoltine, "perpetual species," *D. detecta* and *N. dorsalis*, presumably because of their opportunistic strategies. "Seasonal species" and "perpetual species" with fewer annual generations (*T. minuta*), having specific feeding, oviposition, and substrate requirements, which were altered or destroyed with dethatching, showed population decreases.

All empirical and experimental evidence supports the contention that the complex microstructure and dense thatch of SP combine to form a more heterogeneous and less rigorous resource which subsequently supports a more diverse and specialized assemblage of sap-feeding insects than SAS.

Acknowledgment

I thank B. D. Denno for processing the many samples, P. Barbosa and K. V. Yeargan for helpful comments on the manuscript, E. E. Grissell (Florida Department of Agriculture and Consumer Services), J. L. Herring, J. P. Kramer, A. S. Menke, and D. R. Miller (Systematic Entomology Laboratory, IIBIII, ARS, USDA) for determining the various species of sap-feeders, predators, and parasites, and C. Varnum for typing the final manuscript.

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