

Consumer pressure and seed set in a salt marsh perennial plant community

M.D. Bertness, C. Wise, and A.M. Ellison

Graduate Program in Ecology and Evolutionary Biology, Box G, Brown University, Providence, RI 02912, USA

Summary. Seed predation can be an important determinant of plant success, but has received little attention in wetland plant communities. Here, we examine the role of flower and seed predators in limiting the seed production of the dominant perennial plants in a salt marsh plant community. Of the four perennials investigated, direct ovule loss to consumers ranged from 51 to 80%, resulting in seed set reductions ranging from 50% to over 20-fold. Most losses were due to generalist grazing by the grasshopper, *Conocephalus spartinae*. More species-specific losses were inflicted by planthoppers, and microlepidopteran and dipteran larval seed parasites.

Insect abundance and consumer pressure on flowers and seeds increased over the early summer, peaked in the middle of July, and declined through August, and this temporal pattern was reflected in the natural consumer damage incurred by each of the marsh perennials. *Juncus gerardi* flowers earlier than other marsh perennials and largely escapes heavy consumer losses. *Spartina patens* and *Distichlis spicata* flower in the middle of the summer during the peak consumer activity and incur extremely heavy seed losses. *Spartina alterniflora* flowers late in the summer as consumer pressure is subsiding, which appears to minimize its seed loss. In addition to destroying seeds directly, consumers also markedly reduce the frequency and affect the timing of sexual expression in these plants. In particular, predation drastically reduces the frequency of male flowers, which could lead to pollen limitation of seed set.

Intense flower and seed predation on these marsh perennials may be an important determinant of the success of marsh plant populations as well as a potent selective force on their flowering phenologies and reproductive effort.

Key words: Predispersal seed predation – Seed set – flowering phenology – Salt marsh plants – Grasshoppers

Considerable recent attention has focused on the importance of seed predation in affecting the seed output and recruitment of plants in natural communities. Seed predation by insects, birds, and mammals appears to be extremely common (Salisbury 1942; Janzen 1971; Cavers 1983), and has been shown to significantly lower seed production (Breedlove and Ehrlich 1968; Waloff and Richards 1977; Kinsman 1978) as well as limit juvenile recruitment (Louda 1982a, 1982b). Seed predation has been suggested to limit

the abundance of plants in natural communities (Janzen 1971; Cavers 1983) and operate as a selective force in molding flowering phenologies (Breedlove and Ehrlich 1968; Augspurger 1981) and plant defenses (Janzen 1971). The consequences of seed predation on plant population dynamics and the abundance and distribution of plants in natural communities (Louda 1983, Inouye et al. 1980), however, are not well known (Harper 1977).

Here, we examine the impact of flower and predispersal seed predation on the seed production of the perennial plants that dominate New England salt marshes. Flower and seed predation on marsh plants (Mobberly 1956; Smalley 1960; Silander 1976) and the scarcity of perennial seedlings in marsh communities (Seneca and Broome 1972; Barbor 1981) have both been recognized, but not examined causally. In this paper we examine the temporal and spatial abundance of flower and seed consumers, quantify the temporal and spatial pattern of flower and seed destruction, and assess the consequences of consumer pressure on the seed production of the dominant members of a marsh plant community. This information, while unavailable for most plant communities, is a prerequisite to elucidating the role of seed consumers in generating patterns of abundance and distribution in plant communities as well as understanding the role of seed consumers as selective agents.

Study site and species

The marsh utilized in this study is a small embayment of Smith Cove in Barrington, Rhode Island USA (see Bertness 1984a), typical of many New England salt marsh habitats (Ayers 1950; Nixon 1982). The seaward border is characterized by a band of tall-form *Spartina alterniflora* \approx 5 m wide, above which a band of short-form *S. alterniflora* (Valiela et al. 1978, Bertness 1985) \approx 3 m wide extends to the mean high water line. The area dominated by *S. alterniflora* represents the portion of the marsh that is flooded daily by tides, or the low marsh (Nixon 1982). Immediately above the low marsh (the high marsh, Nixon 1982) a distinct zone of *Spartina patens*, 5–15 m wide, extends to approximately the mean maximum high water line. Above the *S. patens* zone, *Juncus gerardi* dominates the highest reaches of the marsh in a zone 5–20 m wide, which is subject to tidal inundation only during extreme high tides and storms. A fourth perennial plant species, *Distichlis spicata*, is commonly found associated with recently disturbed areas in the high marsh occurring in discrete patches 1–100 m². A complete description of the plant zonation of this commun-

ity and its dynamics is presented elsewhere (Bertness and Ellison, in press). Throughout this paper, areas of the marsh dominated by tall-form *S. alterniflora*, short-form *S. alterniflora*, *S. patens*, *J. gerardi*, and *D. spicata*, will be referred to as the marsh flat, short *Spartina* zone, *Patens* zone, *Juncus* zone, and *Distichlis* areas, respectively (Bertness 1985).

Spartina alterniflora and *S. patens* are protogynous grasses. *S. alterniflora* produces flower spikes with 3 to 19 panicles, each of which bear 12–24 spikelets each capable of producing a single seed. *S. patens* spikes are smaller, producing 1–4 panicles ($x = 2.3 \pm 0.03$, $n = 185$) each of which bears 12–16 spikelets. *Distichlis spicata* is a dioecious grass with sexual expression determined by environmental conditions (Freeman et al. 1976). At our study site *D. spicata* in the *S. patens* zone are almost always male, whereas in the *J. gerardi* zone most are female. Female *D. spicata* spikes are composed of 5 to 44 panicles ($x = 19.1 \pm 0.61$, $n = 195$) each bearing 2 to 6 spikelets. The rush *Juncus gerardi* is protogynous and its inflorescences produce 2 to 22 ($x = 8.8 \pm 0.4$, $n = 500$) flowers each producing ≈ 60 seeds.

Methods

Insect sampling

To examine the spatial and temporal distribution of insect consumers, we sampled insect fauna during the summer of 1985, beginning in mid-May, before the summer insect fauna was apparent, and ending the last week of August, after most insects had become rare. Every 10 days we took 8 sweep net (30 cm diameter) samples in each of the following areas: 1) marsh flat (tall-form *S. alterniflora*); 2) short *Spartina* zone; 3) *Patens* zone, 4) *Juncus* zone, and 5) a large (8 × 8 m) area dominated by *D. spicata*, located in the *Patens* zone. Insects in each sweep sample were sorted to species and counted. Since a grasshopper, *Conocephalus spartinae*, appeared to be the most common flower predator on the marsh, we measured the body lengths (± 1 mm) of all individuals collected and identified them as juveniles, or male or female adults.

Spatial and temporal pattern in consumer pressure

To examine the intensity of consumer pressure on the flowers of the marsh perennials over the course of the summer, we offered undamaged flower spikes to ambient consumers across the marsh from early July to late August 1985 at one to two week intervals. On each date that the experiment was run, 100 undamaged spikes of the test species were collected haphazardly. Twenty spikes were then placed in each of the 5 vegetation areas sampled for insect abundance. Each spike was placed in a 10 ml test tube filled with fresh water. Each test tube was then attached to a bamboo stake (0.5 cm diameter) and implanted in the substrate leaving the spike in a natural position. Experimental spikes were spaced at half-meter intervals in each marsh zone.

These experiments were performed biweekly with three of the marsh perennials (*S. patens*, *D. spicata*, and *S. alterniflora*) as soon as each began flowering and ending when undamaged spikes could no longer be found. *J. gerardi* was tested only once in early July. *S. patens*, *D. spicata*, and *J. gerardi* spikes for the experiment were collected at

the study site, but since undamaged *S. alterniflora* spikes were extremely rare at the study site, *S. alterniflora* spikes for the experiment were collected from a *S. alterniflora* population which was not as heavily damaged by consumers (see Bertness 1984b for a description of this site). For each temporal replication of the experiment, test spikes were offered in each zone and scored *in situ* after 24, 48, and 72 h for insect damage. The damage observed was almost always the chewing of flowers and seeds we had observed being inflicted in the field and laboratory by grasshoppers and planthoppers. Since after 3 days most test spikes in all zones showed signs of insect damage, after 3 days we collected all spikes and scored them under a dissecting microscope for insect damage. For each spike, we counted the number of damaged and undamaged spikelets.

Natural flower damage patterns

Natural consumer damage patterns were quantified by randomly sampling spikes through the flowering season of each species. For *S. patens*, *D. spicata*, and *J. gerardi*, a 0.25 m (0.5 × 0.5 m) quadrat was tossed blindly at 2 m intervals along a transect line 20 times every 7–10 days over the flowering season of each species. Within the quadrat, all spikes were counted and 5 random spikes were collected and scored, as above, for insect damage and sexual condition. Due to the height of *S. alterniflora*, quadrat sampling was not practical and random bunches (25–35) of stems (10/sampling data) were examined at 1 m intervals along a transect line and scored as either flowering or not and 25–40 randomly collected spikes/sampling period were scored for insect damage and sexual condition. At the first sign of dehiscence the above methods were used to collect a random sample of (> 30) seed-heads of each species, and on each, spikelets were scored for insect damage and then dissected and seeds and seed parasites were counted.

To examine the fate of marsh flowers without predators present we bagged individual spikes and constructed insect exclusion cages. Insect exclusion cages were placed in stands of *S. patens* and *D. spicata*. Cages were constructed of aluminum window screen (1 mm mesh) supported on wooden frames. Each cage measured 1 × 1 × 0.3 m (L × W × H), with screening stapled to the frames except for one side of each cage which was attached with velcro to allow repeated access. Light-reduction by the cages was $\approx 20\%$, and did not have a marked effect on the growth, vigor, or flowering of caged plants. Control cages to examine caging effects were similar to the exclusion cages, but without sides. Three exclusion and 2 control cages were placed in the *Patens* zone immediately after *S. patens* had initiated flowering. For *D. spicata*, 3 exclusion and 2 control cages were placed in a *D. spicata* area in the *Patens* zone which supported primarily male individuals and in a *D. spicata* area in the *Juncus* zone which supported primarily female individuals. Exclusion cages were sprayed with a topical insecticide (0.8% butylcarbityl) every 10 days after construction. 10–30 random flowers in each cage were monitored *in situ* weekly for predator damage and sexual condition.

We also individually bagged flower spikes to exclude predators. We bagged 30 incipient *S. patens* spikes, and 30 *Patens* zone and 30 *Juncus* zone *D. spicata* spikes. Bags were made of white nylon wedding veil material (1 mm mesh), measured 15 × 20 cm, and were secured to flower stems with individually numbered plastic ties. Each bag was

MEAN NUMBER OF INSECTS PER SWEEP

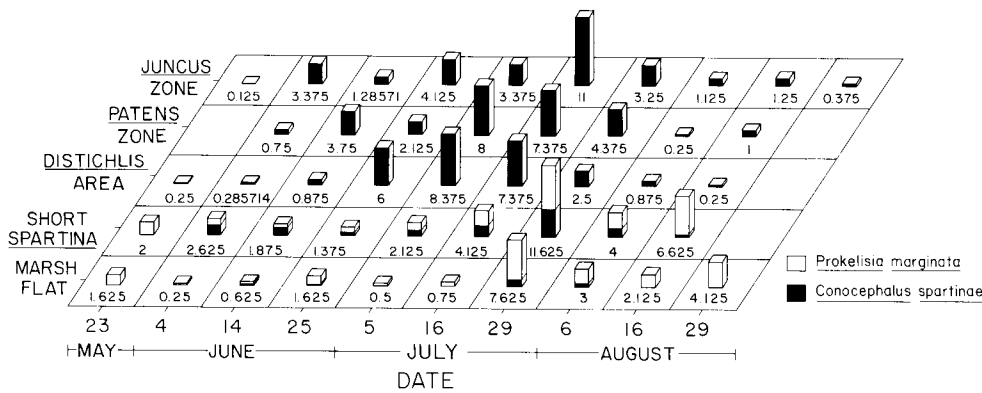


Fig. 1. Results of sweep net sampling of marsh insects giving the mean total number of grasshoppers and planthoppers sampled in 8 sweeps taken in each habitat at each sampling date. Bar shading gives the relative abundance of grasshoppers and planthoppers

supported by a 2 mm wire stake embedded in the substrate at one end and propping the bags open at the other. Bagged spikes were examined daily for insect damage, and sexual condition.

Due to the height of *S. alterniflora* stems (125–175 cm) insect exclusion cages were impractical and not attempted. Instead, we individually marked 30 *S. alterniflora* flower spikes every week from initial emergence the first week of August to the last week of August 1985. We bagged half of these each week. Bags were similar to those described above, but larger (20 × 35 cm) and propped open with wire supports elevated to flower height on bamboo stakes. Marked and bagged *S. alterniflora* spikes were examined every other day for damage and flower condition. We followed weekly cohorts of *S. alterniflora* spikes to examine the effect of emergence time on the performance of *S. alterniflora* flowers, and to avoid biasing our examination of *S. alterniflora* flowers to a single cohort. With *S. patens* and *D. spicata*, caging spikes did not bias our examination to any particular cohort. We examined the effect of emergence time on *S. patens* and *D. spicata* flowers by marking 20 late-emerging spikes of each species the second week of August 1985 and scored them in September for damage and seed set. The performance of these late-emerging spikes was compared with random samples from the populations. In September, immediately before dehiscence, we collected all marked spikes and a random sample of caged flowers and examined them as described above for damage, seed set, and seed parasites.

Results

Insect abundance and distribution

The marsh insect fauna had two abundant species known to consume the flowers of marsh perennials: the planthopper, *Prokelisia marginata*; and the grasshopper *Conocephalus spartinae*. *P. marginata* consumes *Spartina alterniflora* flowers in preference to vegetative tissue (Denno et al. 1980), is small (maximum length ≈ 4 mm) in relation to *S. alterniflora* spikelets, and usually consumes cordgrass flowers by piercing individual spikelets basally and consuming the developing tissue inside (pers. obs.). *C. spartinae* achieves body sizes 4 times that of *P. marginata*, and is a well-known consumer of marsh flowers (Smalley 1960). While smaller individuals attack the basal portion of individual spikelets, larger individuals chew away many spikelets at a time and leave only basal fragments attached to

the stem (pers. obs.). With the exception of a second rare grasshopper species, *Orchelimum concinnum*, no other flower- or seed-consuming insects were apparent on the marsh or found in our sweep net samples. Only one *O. concinnum*, was captured in >250 sweep net samples.

Our survey of flower-consuming insects revealed clear temporal and spatial patterns of abundance. *P. marginata* and *C. spartinae* densities increased through May and June, reached maximum densities during the last two weeks of July, and then declined through the rest of the summer (Fig. 1). *P. marginata* was found exclusively associated with *S. alterniflora* in the low marsh. *C. spartinae*, however, ranged over the entire marsh, and shifted its spatial distribution over the course of the summer (Fig. 1). From May through the middle of July, most grasshoppers were found in the high marsh (91%), while during the remainder of the summer 61% of the grasshoppers sampled were found in the high marsh. This shift in spatial distribution was independent of individual grasshopper size, and coincided with the onset of *S. alterniflora* flowering. Our data probably underestimate the magnitude of this shift in grasshopper abundance from the high to low marsh, since sweep net sampling did not appear to be as efficient in the low marsh as in the high marsh habitat (Vince et al. 1981). Sweep net sampling efficiency in the low marsh was reduced due to the height and robustness of *S. alterniflora*. Since cordgrass is 4–6 times as tall as plants in the high marsh, the volume of the low marsh habitat is much greater/unit surface area in comparison to the high marsh. In addition, the large diameter of *S. alterniflora* stems in contrast to other marsh plants tended to reduce net capture efficiency. Direct observations of grasshopper abundance suggested that relative grasshopper abundance in the low marsh was much higher than our sweep net data indicated. This observation is strongly supported by the extent of grasshopper-inflicted flower damage found in the low marsh habitat (see below).

In addition to the increase in density over the course of the summer (Fig. 1), grasshopper size also increased over the summer (Fig. 2). In May and June only juveniles ranging to 9 mm in length were sampled, while winged adult *P. marginata* were common throughout July and August.

Flowering patterns of the marsh perennials

Of the marsh perennials *J. gerardi* flowers and sets seeds the earliest (Fig. 3A). *J. gerardi* aboveground vegetative growth commences from overwintering rhizomes in mid-March, nearly two months before the spring emergence of

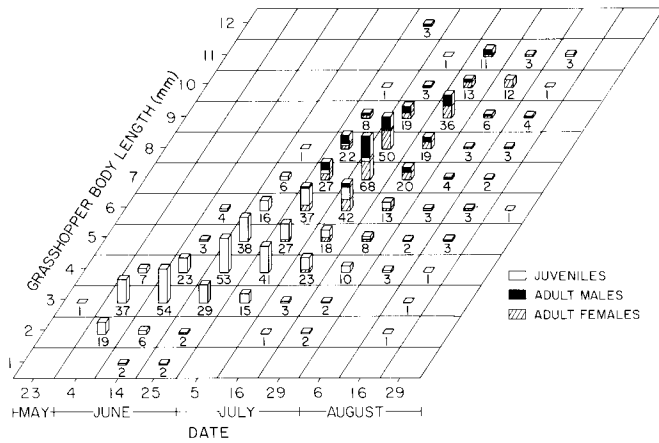


Fig. 2. Size class distribution and sexual condition of grasshoppers, *Conocephalus spartinae*, collected in sweep net samples over the course of the summer of 1985. Data are totals for each size class, pooling all habitats sampled (see Fig. 1)

the remaining marsh perennials. *J. gerardi* flowering begins in the middle of May, continues through early June, with dehiscence of capsules beginning at the end of June. *J. gerardi* inflorescence density ($816/\text{m}^2$) is high in relation to the other marsh perennials, and approximately one in every 30 stems flowers. Virtually all *J. gerardi* set seed before July 15.

S. patens flowering begins in early July (Fig. 3A) with most flowers emerging before August. Inflorescence density is low, reaching a maximum seasonal density of 45.4 ± 9.1 spikes/ m^2 , with approximately one in every 1,300 stems flowering. Flowering is also patchy with heavy flowering ($180/\text{m}^2$) occurring in some areas, while other areas of similar stem heights and densities and at similar tidal heights not producing flowers. In our weekly surveys of *S. patens* spike densities, the minimum coefficient of variation was 91%. In *S. patens* spikes protected from consumers, 7% died without extending flower parts, 3% produced stigmas only, and the remaining 90% initially produced stigmas and then anthers, with considerable viable stigma and anther temporal overlap (Fig. 3B). Once emerged, male parts appeared to produce pollen for only 2–4 days, but we were unable to nondestructively score older males for pollen production. When protected from insect predation, sexual expression in individual *S. patens* spikes is apparent for ≈ 3 weeks (Fig. 3B).

D. spicata began flowering the third week of July, 2 weeks after *S. patens*. *D. spicata* flowers in the *Juncus* zone (males) emerged 7–10 days earlier than those in the *Patens* zone (females). Areas where male and female *D. spicata* individuals co-occurred are extremely rare at our study site. *D. spicata* inflorescence densities in the areas sampled in the *Juncus* zone reached 80.8 ± 13.2 spikes/ m^2 by late August with approximately 1 in every 250 stems flowering; while in the *Patens* zone *D. spicata* patches, densities of 336.8 ± 32.4 spikes/ m^2 were reached by late August with 1 in every 65 stems flowering. The maximum coefficient of variation of *D. spicata* spike density in both the *Juncus* and *Patens* zones was $< 50\%$. *D. spicata* spikes protected from predators had identifiable sexual parts for > 10 days.

Of the marsh perennials, *S. alterniflora* is the last to flower (Fig. 3A). Emergent *S. alterniflora* spikes occurred

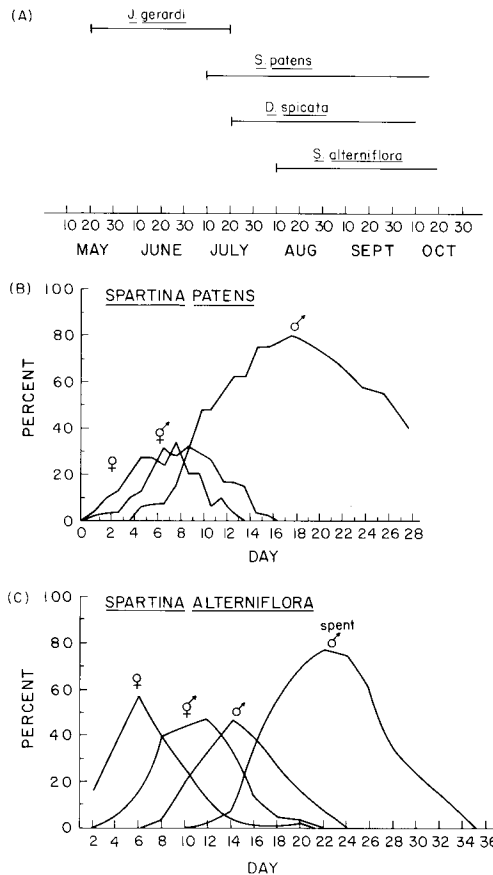


Fig. 3A. Flowering periods of the marsh perennials under consideration. **B** Phenologies of 30 *S. patens* spikes in predator exclusion bags. Spikes were scored daily from emergence (day 0) for the presence of male and female parts. **C** Phenologies of 30 *S. alterniflora* spikes in predator exclusion bags scored every other day for male and female parts

from the first to last week of August, and reached a maximum density of $50/\text{m}^2$ with approximately 1 out of every five stems flowering. Flowering in *S. alterniflora* is relatively homogeneous (C.V. $< 40\%$). Of the sixty bagged *S. alterniflora* spikes examined, 2 died without extending sexual parts, while the rest initially had female parts only, then both viable female and male parts, and then a period where only viable male parts were present (Fig. 3C). Viable anthers were easily distinguished from spent anthers, and viable female/male overlap on an inflorescence was most commonly among panicles, but did occur occasionally within panicles. When protected from predators, sexual expression in individual *S. alterniflora* was apparent for > 3 wks (Fig. 3C).

Spatial and temporal variation in consumer pressure across the marsh habitat

Results of our examination of consumer pressure across the marsh are presented graphically in Fig. 4. Statistically, we evaluated habitat and temporal variation in consumption (proportion of each inflorescence consumed in 3 days) of each species (habitat \times time ANOVA) and compared consumption between species where data was available for two species on ≥ 1 sampling dates (species \times habitat \times time,

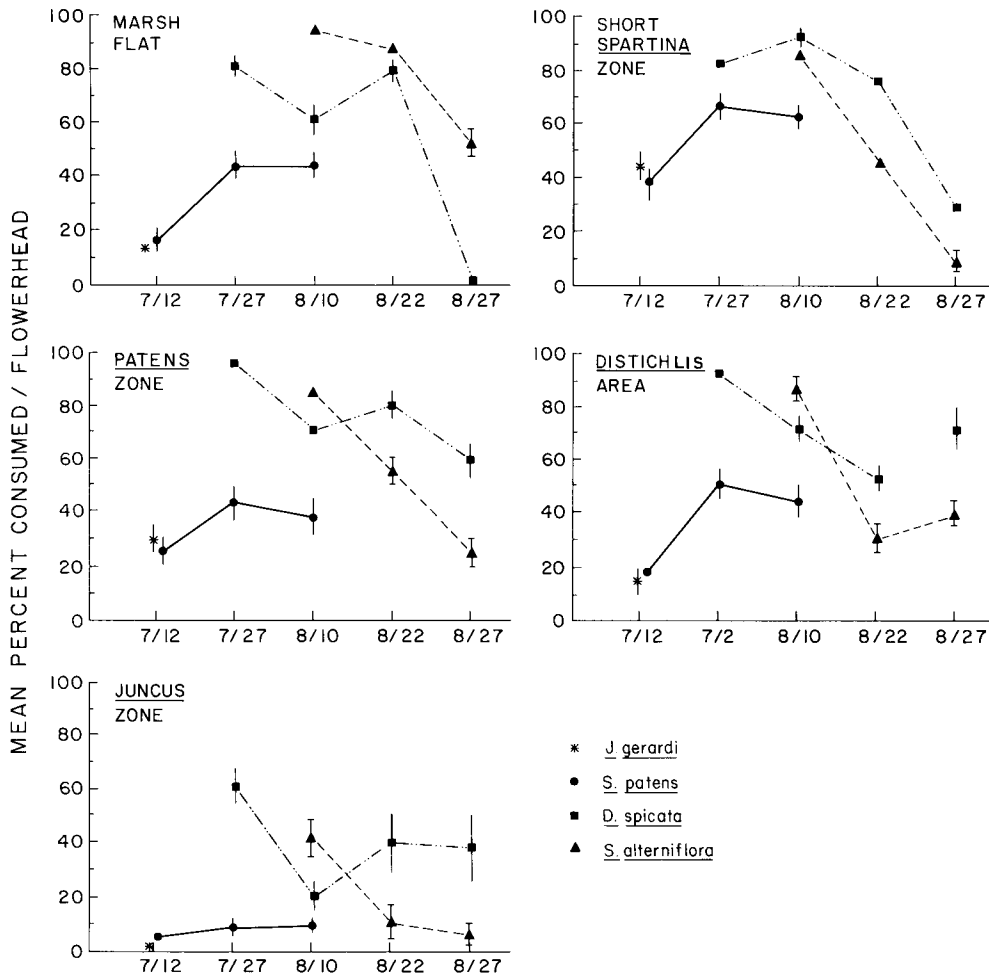


Fig. 4. Results of consumer intensity tests on the spikes of *J. gerardi* (*), *S. patens* (●), *D. spicata* (■), and *S. alterniflora* (▲). Each point represents the mean consumption of 20 spikes over a 3 day test period. Percent consumption was calculated from the proportion of total ovule units/spikes which were eaten by consumers. Standard error bars are given when they exceed symbol size. See text for methodological details and statistics

ANOVA). All analyses were performed on arcsin transformed data to satisfy the assumptions of ANOVA.

Consumption of *J. gerardi* was tested only once, during the second week of July, since up until that time little evidence of flower or seed predation was observed anywhere on the marsh (Fig. 5). At the time the tests were made, *J. gerardi* flowers had senesced and were developing seed capsules, so we tested maturing *J. gerardi* infructescences only 7–10 days prior to dehiscence. $22.3 \pm 2.4\%$ of all capsules presented were eaten in the three day test. Consumption differed significantly ($P < 0.001$, ANOVA) among habitats (Fig. 4), with consumption in the short *Spartina* zone being higher and consumption in the *Juncus* zone being lower than in other marsh habitats tested ($P < 0.05$, Scheffe).

Recently-emerged *S. patens* flowers were tested the second and third week of July and the first week of August (Fig. 4). Consumption of *S. patens* flowers increased over time ($P < 0.001$, time \times zone ANOVA), with flower consumption during the second week of July ($20.1 \pm 2.2\%$) significantly lower ($P < 0.05$, Scheffe) than consumption the fourth week of July ($43.3 \pm 3.2\%$) and the first week of August ($37.5 \pm 2.6\%$). Consumption of *S. patens* flowers also differed spatially ($P < 0.001$ time \times zone ANOVA). Consumption of *S. patens* was greatest in the short *Spartina* zone ($53.6 \pm 3.1\%$) ($P < 0.05$, Scheffe test) least in the *Juncus* zone ($20.6 \pm 2.7\%$) ($P < 0.05$, Scheffe) and intermediate in the *Patens* zone ($37.9 \pm 3.9\%$), the marsh flat ($34.7 \pm 3.4\%$)

and the *Distichlis* area ($34.7 \pm 3.3\%$). Habitat differences in *S. patens* flower consumption were consistent among dates of the experiment ($P > 0.10$, habitat \times date interaction).

D. spicata flowers were offered the third week of July, and the first, third, and last weeks of August (Fig. 4). Consumption of *D. spicata* flowers differed among dates ($P < 0.001$, time \times habitat ANOVA), showing a general decrease over time (July 27, $86.6 \pm 2.4\%$; Aug. 10, $66.5 \pm 2.6\%$; Aug. 22, $72.9 \pm 3.2\%$; and Aug. 29, $51.5 \pm 4.1\%$). Habitat also affected these consumption rates ($P < 0.001$ time \times habitat ANOVA). In results similar to those for *J. gerardi* and *S. patens*, consumption of *D. spicata* flowers was highest in the short *Spartina* zone ($90.5 \pm 1.6\%$), similar in the *Patens* zone ($78.6 \pm 3.0\%$) and *Distichlis* area ($74.6 \pm 3.3\%$), lower on the marsh flat ($55.8 \pm 3.8\%$), and lowest ($36.5 \pm 4.0\%$) in the *Juncus* zone ($P < 0.05$, Scheffe, each case). Habitat, however, did not effect *D. spicata* consumption similarly over time ($P < 0.001$, ANOVA time \times habitat interaction). This reflects that over time, consumption in low marsh habitats dropped off more dramatically than in high marsh habitats (Fig. 4).

S. alterniflora flowers were tested the first, third, and fourth week of August and consumption decreased ($P < 0.001$, time \times habitat ANOVA) over time (Aug. 10, $86.9 \pm 1.8\%$; Aug. 22, $52.5 \pm 3.6\%$; Aug. 29, $33.7 \pm 2.4\%$). Consumption of *S. alterniflora* also varied with habitat ($P < 0.001$, time \times habitat ANOVA) showing a general decrease

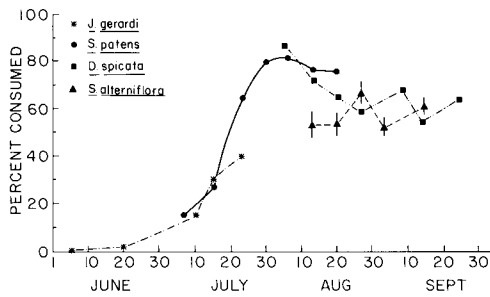


Fig. 5. Mean percent spike consumption of *J. gerardi* (*), *S. patens* (●), *D. spicata* (■), and *S. alterniflora* (▲) sampled randomly when each species was in flower. Percent consumption was calculated from the proportion of the total ovule units/spike which had been eaten by consumers. Standard error bars are given where they are larger than the symbols. Sample sizes ranged from 30 to 100 spikes/data (see methods)

from low to high marsh habitats (marsh flat $82.6 \pm 2.6\%$; short *Spartina* $69.9 \pm 3.3\%$; *Patens* zone $56.5 \pm 4.3\%$; *Distichlis* area $47.4 \pm 4.2\%$; and *Juncus* zone $17.1 \pm 3.3\%$). The interaction between the date of the experiment and habitat was not significant for *S. alterniflora* flower consumption ($P > 0.05$, habitat \times date ANOVA interaction). The higher consumption of *S. alterniflora* on the marsh flat in contrast to the other species tested may reflect a strong preference of planthoppers for *S. alterniflora* in comparison to the other marsh grasses (Fig. 4).

Interspecific comparisons were made on percent consumption data in cases where 2 species were tested on one or more dates (Fig. 4). Consumption of *J. gerardi* and *S. patens* over the same 3 day period did not differ significantly ($P > 0.40$, species \times habitat ANOVA, $P > 0.50$, interaction). In contrast, consumption of *S. patens* and *D. spicata* on the 2 dates that they were tested simultaneously, was significantly ($P < 0.001$ species \times time \times habitat ANOVA) higher on *D. spicata* ($74.4 \pm 4.5\%$) than on *S. patens* ($41.1 \pm 3.2\%$). This difference was not affected by habitat ($P > 0.05$, species \times habitat interaction), but was significantly influenced ($P < 0.005$, species \times time interaction) by the date of the experiment. These data suggest that *D. spicata* may be preferred over *S. patens* by marsh flower consumers. Consumption of *S. alterniflora* and *D. spicata* flowers can be compared on 3 test dates (Fig. 4). Overall consumption of these species did not differ significantly ($P > 0.10$ species \times time \times habitat ANOVA), but both test date (species \times time interaction) and habitat (species \times habitat interaction) significantly ($P < 0.001$, ANOVA) affected the comparative consumption of these species. This reflects that *S. alterniflora* flowers are eaten more heavily than *D. spicata* flowers in the low marsh, while *D. spicata* flowers are eaten more heavily than *S. alterniflora* flowers in the high marsh, and that this relative difference increases over time (Fig. 4).

A number of generalizations can be made on the basis of the flower predation tests. First, flower predation intensity on the marsh increases early in the summer, peaks in late July and early August, and then drops off at the end of the summer. This pattern is consistent with most of the tests made (Fig. 4), and reflects the abundance of flower consumers on the marsh (Fig. 1). Second, flower predation generally decreases from high marsh (*Juncus* zone) to low marsh habitats (short *Spartina* zone and marsh flat). For all species tested consumer pressure was the least in the

Juncus zone and the highest in low marsh habitats (Fig. 4). This also reflects the abundance of flower consumers across the marsh (Fig. 1). Finally, while consumer preferences may exist among flower-types, e.g., *D. spicata* may be preferred over *S. patens*, flowers of all species were attacked and heavily damaged. Most variation in consumer pressure on these flowers appears to be the result of spatial and temporal variation in consumer abundance, rather than specific consumer preferences for particular flower types.

Natural flower damage in the marsh plant community

Results of our sampling of each of the marsh perennials over their flowering seasons to assess consumer damage are given in Fig. 5. Little ($< 5\%$) predation was observed on *J. gerardi* flowers before the second week of July when adult grasshoppers appeared in the marsh (Fig. 2). Consumer damage to *J. gerardi* increased over time until dehiscence, when 42% of the seed capsules had been destroyed by chewing insects. Damaged *J. gerardi* almost always had more than half of the wall of the capsule chewed away, and the developing seeds inside removed. Grasshoppers inflicted this type of damage to *J. gerardi* in the field and laboratory (pers. obs.) Parasitic moths (*Coleophora* spp.), destroyed an additional 13% of the *J. gerardi* capsules, leaving round bore holds ≈ 1.5 mm in diameter in empty capsules.

Damage to *S. patens* spikes began immediately after flowering began (Fig. 5), and was almost exclusively characterized by the chewing damage inflicted by grasshoppers. *S. patens* spike damage increased over time, and by the last week of August all spikes sampled ($n = 84$) were damaged, with individual spike damage averaging 81%. Spikes sampled during the second and third weeks of August tended to have less damage than at earlier sampling dates (Fig. 5), suggesting that late emerging spikes may sustain less damage than earlier emerging ones.

Damage to *D. spicata* spikes is given combining samples from the *Juncus* and *Patens* zones, since while damage did differ somewhat between the areas, they revealed similar temporal patterns. Damage to *D. spicata* spikes often occurred before flower emergence. In over half (54% $n = 96$) of the *D. spicata* spikes sampled in the first week of August, preemergent flowers, identifiable as swellings on incipient flower spikes, had been chewed away exposing totally consumed, immature flowers. Grasshoppers were responsible for this damage. Early emerging *D. spicata* flowers were heavily damaged by consumers; an average of 85% of each spike sampled the first week of August was destroyed. *D. spicata* flower damage, however, decreased over time (Fig. 5) again suggesting that late emerging flowers may escape heavy predation. Just prior to dehiscence, all *D. spicata* sampled ($n = 80$) were damaged with damage/spike averaging 63% (Fig. 5).

Damage to *S. alterniflora* spikes was characterized by both the removal of many adjacent spikelets characteristically inflicted by adult grasshoppers, and the chewing of individual spikelets characteristically inflicted by smaller grasshoppers and planthoppers. *S. alterniflora* spikes were damaged heavily (54%) as they emerged, and like *D. spicata*, many were chewed open by grasshoppers prior to emergence. Damage to *S. alterniflora* spikes remained relatively constant from emergence to the end of September (Fig. 5). All spikes were damaged to some extent by the

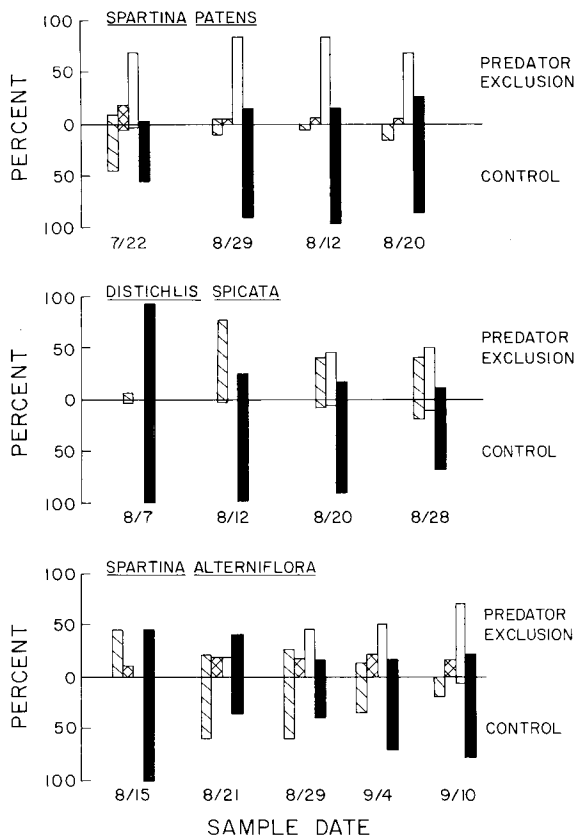


Fig. 6. Sexual condition of *S. patens*, *D. spicata* and *S. alterniflora* spikes in control areas exposed to predators and in predator exclusion cages and/or bags. Sample sizes for each sampling date and species were >25 for both controls and predator exclusions. Lined bars represent female spikes; crosshatched bars, spikes that were simultaneously female and male; open bars, male spikes; and solid bars, spikes without signs of male or female parts. See text for details

middle of September ($n=60$) with damage/spike averaging $59.2 \pm 4.8\%$.

A predictable consequence of the heavy consumer damage to the flowers of these species is that consumer pressure affects the sexual expression of their populations. This may result directly when spikelets are consumed before expressing sexuality, or indirectly when portions of an inflorescence are destroyed, affecting the health of adjacent undamaged spikelets. In addition, grasshoppers commonly forage on flowers removing extended stigmas and anthers without actually chewing into spikelet tissue (pers. obs.).

The influence of consumers on the sexual expression of marsh perennials can be examined by comparing sexual expression of control flowers with flowers protected from consumers pooled over their flowering seasons. For *S. patens* (Fig. 6), exposure to predators significantly ($P < 0.001$, G-test) affected sexual expression. In caged *S. patens*, 82% ($n=256$) of the spikes sampled over the summer had exposed anthers, while in control spikes ($n=564$) $<2\%$ had anthers. Conversely, 84% of the control spikes showed no sign of sexual expression, while $<15\%$ of *S. patens* protected from consumers did not have male or female parts. Exposure to consumers similarly ($P < 0.001$, G-test) affected sexual expression in *D. spicata* (Fig. 6). Of the *D. spicata* spikes from predator exclusion cages, 31% ($n=359$) had

no signs of sexual parts, while with spikes exposed to consumers ($n=625$) 66% of the flowers were without male or female parts. Comparing bagged and unbagged *S. alterniflora* (Fig. 6), 63% ($n=130$) of the unbagged *S. alterniflora* spikes revealed no signs of sexual expression, while only 24% ($n=252$) of the bagged spikes were found lacking male or female parts ($P < 0.001$, G-test).

Predators also influenced temporal patterns of sexual expression. In *S. patens* exposed to consumers, sexual expression peaked at first emergence and then again late in the flowering season in contrast to relatively high sexual expression throughout the flowering season in spikes protected from consumers (Fig. 6). In *D. spicata*, a similar pattern is evident with sexual expression increasing over time in controls in contrast to continuous sexual expression in spikes protected from consumers (Fig. 6). Finally, in *S. alterniflora* spikes, functional males were not observed until late in the flowering season in controls, but were common throughout the flowering season in spikes protected from predators. These temporal patterns in the sexual expression of flowers exposed to consumers suggests that at the end of the growing season when consumer pressure declines (Fig. 4) sexual expression increases. Consumer pressure, then, not only reduces the overall expression of sex, but also has strong effects on the timing of sexual expression in these populations. In particular, consumers dramatically reduced the frequency of male flowers in each of these grasses (Fig. 6).

Seed set

To evaluate seed set, seed/ovule ratios were compared among treatments using arcsin transformed data. Comparisons were made on seed/ovule ratios calculated using the total number of ovules initiated, including those destroyed by consumers. Seed/ovule ratios calculated considering only intact ovules (ovules not eaten by predators or parasites) and seed output/spikes are also given. Evaluation of these later two measures of seed production, in general, are in total agreement with the analysis presented.

S. patens spikelet loss to chewing insects differed significantly ($P < 0.0001$, ANOVA) among the treatments examined for seed set, decreasing from transect spikes ($77.5 \pm 3.7\%$) to late spikes ($13.3 \pm 3.7\%$) and caged spikes ($9.6 \pm 3.0\%$), with no losses to chewing insects occurring in bagged spikes. On spikelets not destroyed by chewing insects, however, losses to dipteran seed parasites also differed significantly among treatments ($P < 0.001$, ANOVA), and were highest in bagged ($29.1 \pm 3.0\%$) and late ($23.0 \pm 2.8\%$) spikes, and minimal in transect ($5.1 \pm 1.9\%$) and caged ($0.8 \pm 0.9\%$) spikes. While this suggests that flowers not attacked by chewing insects are more likely to be parasitized and that exclusion bags did not reduce parasite losses, total ovule loss to both consumer types significantly reflected ($P < 0.001$, ANOVA) our efforts to reduce *S. patens* consumer losses. Total losses (predator + parasite) in the transect spikes (78.5 ± 3.7) were higher ($P < 0.001$, Scheffe test, both cases) than for either late ($32.5 \pm 3.9\%$) or bagged ($28.5 \pm 4.7\%$) spikes, while caged spikes had less ($P < 0.001$, Scheffe test) total losses ($10.8 \pm 4.1\%$) than any other treatment.

Seed production varied dramatically ($P < 0.001$, ANOVA) among the *S. patens* treatments (Fig. 7). Less than 1% ($0.6 \pm 0.1\%$) of the ovules on transect spikes produced

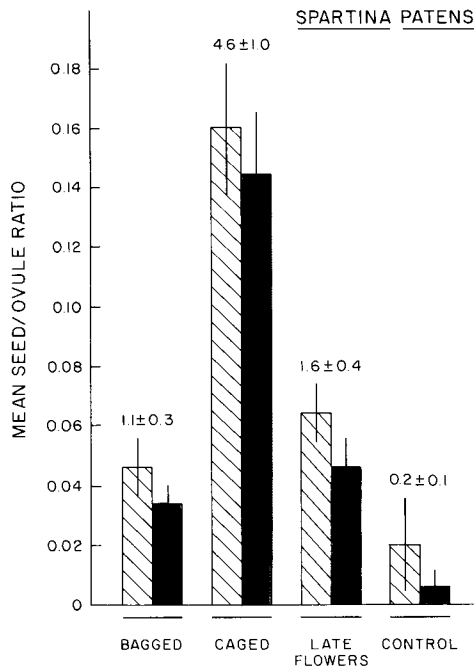


Fig. 7. Seed output of *S. patens* seedheads from control samples, late-emerging spikes, and spikes which were bagged or caged to exclude insect flower predators. Sample sizes are >15 for each cage and vertical bars are standard errors. Lined bars represent seed/ovule ratios calculated including only intact ovules that showed no direct consumer damage, solid bars are seed/ovule ratios calculated on the basis of all initiated ovules, including those destroyed by consumers. Mean seed production/spike (\pm se) for each treatment is given over the error bars. See text for statistical treatment

seeds, fewer ($P < 0.001$, Scheffe test) than in any other treatment. Seed production did not differ ($P < 0.50$, Scheffe test) between late ($4.6 \pm 1.3\%$) and bagged ($3.4 \pm 1.0\%$) spikes, and was highest ($P < 0.001$, Scheffe test) in caged spikes ($14.5 \pm 2.9\%$). Caged spikes produced 23 times as many seeds as transect spikes exposed to consumers (Fig. 7).

Consumer damage on the female *D. spicata* examined for seed production differed ($P < 0.001$, ANOVA) among treatments, with losses on control spikes ($58.5 \pm 3.7\%$) higher ($P < 0.01$, Scheffe test) than on late spikes ($37.1 \pm 5.4\%$), whereas losses on spikes in bags ($3.8 \pm 1.3\%$) and in cages ($0.8 \pm 1.0\%$) were negligible. Seed loss to larval parasites was less than 1% overall, and did not differ among treatments.

Seed production differed dramatically ($P < 0.001$, ANOVA) among *D. spicata* treatments (Fig. 8). Late spikes produced more seeds/ovule ($0.44 \pm 0.1\%$) than caged spikes ($0.25 \pm 0.1\%$), $P < 0.05$, Scheffe test, which produced more seeds/ovule ($P < 0.05$, Scheffe) than either control ($0.09 \pm 0.04\%$) or bagged ($0.04 \pm 0.02\%$) spikes. Similar results are obtained analyzing seed/ovule ratios based on undamaged ovules only and on seed production/spike. A noteworthy exception, however, is that seed production/spike did not differ between late and caged spikes in spite of a twofold difference in their seed/ovule ratios (Fig. 8). This disparity was the result of late spikes producing fewer ovules than earlier spikes. The low seed set of bagged spikes also indicated that bagging interfered with seed production in *D. spicata*. Caging *D. spicata* from consumers, however,

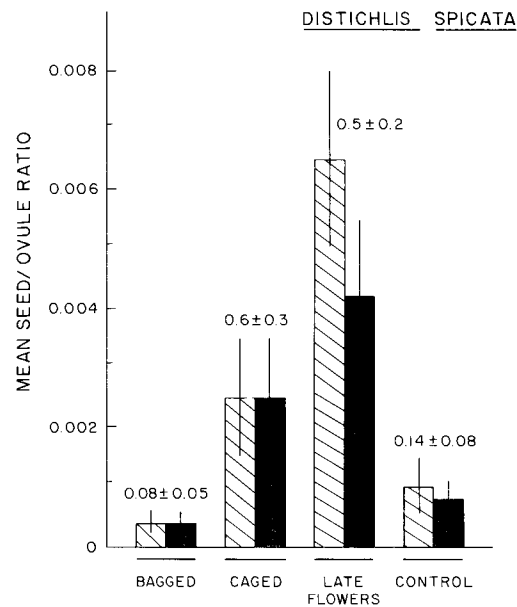


Fig. 8. Seed output of female *D. spicata* spikes from control samples, late-emerging spikes, and spikes which were bagged or caged to exclude insect flower predators. Sample sizes for each case >25 . Symbols as in Fig. 7. See text for details and statistical treatment

resulted in increased seed output/spike by over a factor of 4 in comparison to transect spikes.

S. alterniflora predator exclusion bags reduced damage by chewing insects and seed parasites. Damage by chewing insects was negligible ($<3\%$) on bagged spikes from all cohorts, whereas insect damage on unbagged spikes decreased significantly ($P < 0.001$, ANOVA) from the flowers marked the first week of August ($73.1 \pm 5.6\%$) to later cohorts (Aug. 14, $44.1 \pm 7.6\%$; Aug. 20, $50.1 \pm 6.6\%$; Aug. 28, $52.9 \pm 7.8\%$). Similarly, while few dipteran larval seed parasites ($<2\%$ of ovules) were found on bagged spikes, in unbagged spikes, more ($P < 0.01$, ANOVA) ovules on spikes marked the first week of August ($21.0 \pm 4.0\%$) were parasitized than on later cohorts (Aug. 14, $8.3 \pm 1.6\%$; Aug. 20, $9.4 \pm 2.5\%$; Aug. 28, $9.8 \pm 2.1\%$). As a result of both predator and parasite losses, bagged spikes lost $<5\%$ of their ovules, while unbagged spikes lost $>50\%$ of their ovules (Aug. 7, $79.2 \pm 4.3\%$; Aug. 14, $49.1 \pm 6.9\%$; Aug. 20, $60.9 \pm 5.7\%$; Aug. 28, $59.1 \pm 6.5\%$).

Protecting *S. alterniflora* spikes from consumers increased ($P < 0.001$, ANOVA) the overall proportion of ovules producing seeds (Fig. 9) by nearly a factor of 5 ($30.7 \pm 3.4\%$ for bagged spikes, $6.5 \pm 1.3\%$ for unbagged spikes), and increased individual spike seed set (66.0 ± 9.0 /bagged spike; 15.2 ± 3.6 /unbagged spike) by over a factor of 4. Spike emergence time (Fig. 9) significantly affected the proportion of ovules producing seeds ($P < 0.001$, ANOVA) and this temporal effect on seed production was independent ($P > 0.30$ ANOVA, treatment \times time interaction) of whether or not spikes were exposed to consumers. Spikes emerging the first week of August produced fewer seeds than spikes that emerged in the following week, and seed production of spikes emerging during the following weeks declined over time (Fig. 9). Transect spikes had a lower seed output (2.8 ± 1.4 seeds/spike) and fewer ovules produced seeds ($18.9 \pm 0.5\%$) than unbagged marked spikes ($P < 0.01$, ANOVA). This appeared to be due to higher

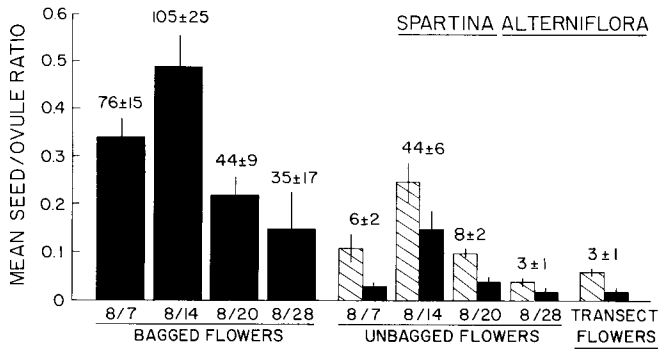


Fig. 9. Seed output of emerging *S. alterniflora* spikes which were individually marked and either bagged to exclude insect predators or left exposed to predators, at weekly intervals in August 1985. Minimum sample size is 15 for each treatment and date. Symbols are as in Fig. 7. Data are also given for random transect spikes ($n=45$). See text for details and statistical treatment

consumer losses on transect spikes ($78.4 \pm 2.8\%$) than on marked stems ($63.7 \pm 3.2\%$). The transect spikes are probably more representative of the *S. alterniflora* population at the study site, since they were individuals collected randomly from the population. We marked spikes only on the high marsh border of the *S. alterniflora* zone so that we could repeatedly monitor them without trampling surrounding vegetation.

Discussion

Our results demonstrate that predispersal consumption of the flowers and seeds of these salt marsh perennials dramatically affects seed production (Table 1), and consequently may play an important role in the population and community dynamics of marsh plants. Most of the consumer pressure documented was attributable to the grasshopper, *Conocaphalus spartinae*, which appears to specialize on perennial flowers and seeds, but not to have marked preferences for the flowers of any one perennial species. Grasshopper densities rise in the spring following the hatching of overwintering eggs, reach peak densities by the middle of the summer, and then decline over the remainder of the summer (Fig. 1). The grasshopper population also shifts from high to lower levels of the marsh over the summer. This pattern of grasshopper abundance is mirrored accurately in the temporal and spatial pattern of consumer pressure on perennial

marsh flowers, suggesting that grasshoppers are the major flower and seed predators in this community. Flower and seed consumption is negligible early in the summer before the appearance of adult grasshoppers (Figs. 2 and 4), but as grasshopper numbers increase and particularly as large winged adults become common, consumer losses to available flowers and seeds increase dramatically. At the end of the summer, as grasshopper numbers decrease, consumer losses show a parallel decline (Fig. 4). The tight fit between the spatial and temporal pattern of grasshopper abundance and consumer losses, coupled with generalist consumption of flowers and seeds by grasshoppers, suggest that predation on the flowers of these species is primarily a function of their temporal and spatial availability, rather than on their species identity. This appears to be true in spite of other, more specialized, species-specific flower consumers and seed parasites in the community.

Juncus gerardi begins flowering in the middle of May, nearly two months before the appearance of any other flowers on the marsh (Fig. 3). In the absence of most consumers, *J. gerardi* flowers and seed capsules sustain minimal damage before July when adult grasshoppers appear on the marsh. Most *J. gerardi* capsules dehisce by the middle of July, and are exposed to grasshopper predation for only 2–3 weeks, but during this short period lose $>40\%$ of their seeds to grasshoppers. Moth seed parasites account for an additional 13% loss of the *J. gerardi* seed crop. Consumers destroy 10–15% of the *J. gerardi* seeds available each week once heavy consumer pressure begins in July (Fig. 5), suggesting that if *J. gerardi* began flowering just 3 weeks later in the spring, its losses to consumers would approach 100%. The success of *J. gerardi* seed production (Table 1) appears to result from early flowering, allowing it to set seed before sustaining heavy consumer losses.

Spartina patens flowering begins in early July, as adult grasshoppers are becoming common and consumer pressure on flowers is increasing (Fig. 4). Consumer losses to *S. patens* attributable to grasshoppers rise rapidly, reaching 80% by August and ultimately reduce seed set by well over an order of magnitude (Fig. 7). Seed parasites also contribute significantly to *S. patens* ovule loss. Consumer damage to *S. patens* spikes reduces sexual expression in the population, and in particular, limits the number of spikes which reach the male phase of their protogynous phenology (Fig. 6). As a result of reduced consumer pressure, late-emerging *S. patens* spikes incur less consumer damage, exhibit increased sexual expression (Fig. 6), and set nearly an order

Table 1. Summary of flower and seed set characteristics of the marsh perennials

Species	Spikes/m ²	Consumer loss/spikes	Seed/ovule controls (predators removed)	Seeds/spikes controls (predators removed)	Estimated Seed set/m ² controls (predators removed)	Observed ^a seedling density/m ²
<i>Juncus gerardi</i>	816 ± 80	54%	41%	270	210,320	508 ± 176
<i>Spartina patens</i>	45 ± 9	80%	0.63% (14.5%)	0.19 (4.6)	8.5 (207)	8.4 ± 4.4
<i>Distichlis spicata</i>	80 ± 13 (J. gerardi zone)	51%	0.12% (0.25%)	0.14 (0.60)	11 (48)	4.4 ± 2.0
<i>Spartina alterniflora</i>	50 ± 5	68%	1% (30%)	2.8 (66)	140 (3,300)	60 ± 10

^a Data from Bertness and Ellison (in press); seedling survivorship over a single growing season in “safe sites” (*sensu* Harper 1977) is ~50% for each species

of magnitude more seeds than flowers produced earlier in the summer (Fig. 7).

Distichlis spicata begins flowering late in July when consumer pressure on flowers is at its peak. *D. spicata* spikes are initially hit extremely hard by consumers, but as the flowering season progresses, damage to *D. spicata* spikes decreases (Fig. 5). As was the case with *S. patens*, consumers markedly reduce sexual expression of *D. spicata* (Fig. 6), and as consumer pressure subsides in the late summer, sexual expression increases resulting in late-flowering females setting nearly five times the seeds as early-flowering ones (Fig. 8).

Spartina alterniflora flowering begins in early August, later than any of the other marsh perennials, and continues into early September. Predation on *S. alterniflora* flowers decreases over its flowering season as its predators, *P. marginata* and *C. spartinae*, decrease in abundance (Figs. 1 and 4). In spite of beginning flower production as consumer populations are declining, *S. alterniflora* still sustains heavy losses to consumers, apparently since late in the summer most consumers in the community are found on *S. alterniflora* (Fig. 1). Total *S. alterniflora* seed production losses to consumers are over an order of magnitude (Table 1), and consumers severely limit the expression of male sexuality (Fig. 6) in the population. Consumer pressure on *S. alterniflora*, however, decreases over its flowering season (Fig. 4), suggesting that if it flowered earlier, seed production losses to consumers would be even more severe.

The strong effects exerted by consumers on the sexual expression of the grasses we have studied (*S. patens*, *S. alterniflora*, and *D. spicata*) may have important population repercussions. By temporally shifting the abundance of viable flowers later in the growing season (Fig. 6), predation could result in late-emerging flowers contributing the majority of sexual propagules to the population. The relatively high seed set of late emerging *S. patens* (Fig. 7) and *D. spicata* (Fig. 8) flowers supports this. In addition, by more markedly reducing the abundance of male flowers in comparison to female flowers (Fig. 6), heavy consumer pressure could result in pollen availability limiting seed set in these species. In preliminary investigations we have found that in at least one of the protogynous grasses (*S. alterniflora*) pollen availability limits seed set by > 50%, in spite of self-compatibility (unpublished data).

While our data are the first of their kind to document the impact of consumers on the seed production of marsh perennials, the intense consumer pressure that we report appears to be common in salt marsh communities in southern New England (pers. obs.). Heavy consumer damage on perennial marsh flowers has been casually noted all along the east coast of North America (Mobberly 1956, Smalley 1960), and is most likely common.

By severely reducing seed set, consumer pressure on perennial marsh flowers may have a major impact on their population dynamics as well as potentially serve as a powerful selective force. Consumer pressure of this magnitude could select for temporal adjustments in the phenologies of marsh perennials to minimize heavy consumer losses of sexual propagules, as well as decreased investment of these plants to sexual reproduction. *J. gerardi* and *S. alterniflora* appear to reduce consumer losses of sexual propagules by flowering earlier and later, respectively, than the peak abundance of consumers, and their flowering patterns may reflect that consumer pressure has selected for phenologies

that maximize the production of sexual propagules. Our data on *S. patens* and *D. spicata* which flower in the middle of the summer under heavy consumer pressure, show that late emerging flowers minimize losses to predators and set 4 to 10 times as many seeds as individuals in the population that flower earlier. If flowering times have a genetic basis and successful seedling establishment occurs, this could result in strong selective pressure for later flowering. Interestingly, *S. alterniflora* populations near our study site which are insular and are not subject to heavy insect flower consumption have begun flowering 2–3 weeks before adjacent marsh populations for the last 3 years (pers. obs.).

The unusually low seed/ovule ratios of these marsh perennials could also be the product of natural selection driven by consumer pressure. *J. gerardi* and *S. alterniflora*, both partially escape consumers temporally, and have seed/ovule ratios (41% and 30%, respectively) that do not deviate markedly from 50%, the average for perennial species (Weins 1984). In contrast, even with the proximate influence of consumer losses factored out (Table 1), *S. patens* (14.5%) and *D. spicata* (0.25%) have unusually low seed/ovule ratios. Since these species can reproduce vegetatively by investing in rhizomes as well as sexually, these low seed/ovule ratios could reflect consumer pressure on flowers selecting for vegetative expenditures at the expense of a lower investment into sexual reproduction. Lower investment into sexual reproduction by marsh perennials exposed to heavy predation may also be reflected in two other measures of sexual reproductive effort: stem flowering frequency, and potential seed output/spike. While 20% of *S. alterniflora* and 3.3% of *J. gerardi* stems flower, < 0.1% of *S. patens* and only 1.5% of *D. spicata* stems flower at our study site. In addition, maximum seed output/spike (maximum number of initiated ovules/spike) is much greater in *J. gerardi* (1320) and *S. alterniflora* (456) than in *S. patens* (64) and *D. spicata* (264). We suggest that the low seed/ovule ratios, frequency of flowering, and potential seed output of *S. patens* and *D. spicata* may reflect that heavy flower consumer pressure has selected for reduced sexual reproductive effort in these species.

Dramatic reduction in seed production due to consumer pressures may also have a number of important and largely unexplored consequences on perennial marsh plant populations and the dynamics of marsh plant communities. By limiting seed production, consumers may minimize the importance of seedlings in marsh plant dynamics, amplify the importance of adult clonal interactions in determining the success of marsh plants and the interspecific spatial patterns of marsh plant communities, and reduce the genetic diversity of marsh plant populations.

Acknowledgements. We thank Beth Farnsworth, Scott Metcalfe, Kristen Schroeder, and Noel Gurwick for field assistance and Annie Schmidt and Scott Metcalfe for comments on the manuscript. Special thanks go to the residents of Rumstick Cove for allowing us access to the field site. This work was supported by grants from the National Science Foundation (BSR 83-13303 and BSR 85-16992).

References

- Augspurger CK (1981) Reproduction synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775–788

- Ayers JC (1959) The hydrography of Barnstable Harbor, Massachusetts. *Limnol Oceanog* 4:448-462
- Barbor MC (1981) Belowground interactions among three salt marsh plants. Dissertation Johns Hopkins University, Baltimore, MD, USA
- Bertness MD (1984a) Ribbed mussels and the productivity of *Spartina alterniflora* in a New England salt marsh. *Ecology* 65:1794-1807
- Bertness MD (1984b) Habitat and community modification by an introduced herbivorous snail. *Ecology* 65:370-381
- Bertness MD (1985) Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* 66:1042-1055
- Bertness MD, Ellison AM (1986) Determinants of pattern in a New England salt marsh plant community. *Ecology* (in press)
- Breedlove DE, Ehrlich PR (1968) Plant-herbivore coevolution: Lupines and Lycaenids. *Science* 162:671-672
- Cavers PB (1983) Seed demography. *Can J Bot* 61:3578-3590
- Denno RF, Raupp MJ, Tallamy DW, Reichelderfer CF (1980) Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper, *Prokelisia marginata* (Homoptera: delphacidae). *Ecology* 61:859-867
- Freeman DC, Klikoff LG, Harper KT (1976) Differential resource utilization by the sexes of dioecious plants. *Science* 193:597-599
- Harper JL (1977) Population biology of Plants. Academic Press, London
- Inouye RS, Byers GS, Brown JH (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61:1344-1351
- Janzen DH (1971) Seed predation by animals. *Ann Rev Ecol Syst* 4033:465-483
- Kinsman S (1978) Impact of an herbivore (*Haliodines nyctaginella*: Lepidoptera) upon fitness of a prairie plant (*Mirabilis birsuta*: Nyctaginaceae). *Bull Ecol Soc America* 59: 109
- Louda SM (1982a) Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecol Mono* 52:25-41
- Louda SM (1982b) Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *J Ecol* 70:43-53
- Louda SM (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climate gradient. *Ecology* 64:511-521
- Mobberly DG (1956) Taxonomy and distribution of the genus *spartina*. *Iowa State College J Sci* 30:471-574
- Nixon SW (1982) The ecology of New England high salt marshes: a community profile. U.S. Fish and Wildlife Service, Washington, DC
- Salisbury EJ (1942) The Reproductive Capacity of Plants: Studies in Quantitative Biology. Bell, London, England
- Seneca ED, Broome SW (1972) Seedling response to photoperiod and temperature by Smooth Cordgrass, *Spartina alterniflora*, from Oregon Inlet, North Carolina. *Ches Sci* 13:212-235
- Silander JA (1976) The genetic basis of the ecological amplitude of *Spartina patens* on the Outer Banks of North Carolina. PhD Dissertation. Duke University, Durham, North Carolina, USA
- Smalley AE (1960) Energy flow of a salt marsh grasshopper population. *Ecology* 41:672-677
- Valiela I, Teal JM, Deuser WG (1978) The nature of growth forms in the salt marsh grass, *Spartina alterniflora*. *Amer Nat* 112:461-470
- Vince SW, Valiela I, Teal JM (1981) An experimental study of the structure of herbivorous insect communities in a salt marsh. *Ecology* 62:1662-1678
- Waloff N, Richards OW (1977) The effect of insect fauna on growth, mortality and natality of broom, *Sarothammus scoparius*. *J App Ecol* 14:787-798
- Weins D (1984) Ovule survivorship, broad size, life history, breeding systems, and reproductive success in plants. *Oecologia (Berlin)* 64:47-53

Received February 18, 1986