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Impact of High Herbivore Densities on Introduced Smooth Cordgrass, *Spartina alterniflora*, Invading San Francisco Bay, California

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ABSTRACT: ***Spartina alterniflora*, smooth cordgrass, invading San Francisco Bay, California (USA), is attacked by high densities of a plant hopper, *Prokelisia marginata*, and a mirid bug, *Trigonotylus uhleri*. Both herbivores are sap-feeders. We investigated the impact of these herbivores on *S. alterniflora's* growth rate, vegetative spread, and seed production by manipulating herbivore densities in the field and in a greenhouse. Herbivore densities in the field peaked in early fall, with *P. marginata* averaging more than 300 individuals per mature culm of *S. alterniflora* (about 100,000 per m^2) and *T. uhleri* densities exceeding 10 per culm (about 3,000 per m^2). Field reductions of herbivore densities by approximately 70% with insecticidal soap did not result in greater vegetative growth rates or lateral spread of plants; plants grew vigorously with the highest densities of insects. In the greenhouse study, conducted with seedlings, herbivory significantly reduced plant mass and tiller number in some but not all replicate herbivory treatments. In both field and greenhouse, there were significant differences between some clones' growth rates independent of herbivory. Inflorescence production in the field was not affected by reduced-herbivory treatments. Seed set was low under conditions of both natural and reduced herbivory, averaging 0.4%. Despite densities of *P. marginata* and *T. uhleri* that are much higher than typically observed in areas where *S. alterniflora* is native, herbivory by these particular insects appears to have little impact and in unlikely to limit *S. alterniflora's* spread through San Francisco Bay.**

Introduction

Spartina alterniflora Loisel, a perennial salt marsh grass native to the Atlantic Coast of North America, has been introduced to estuaries around the world (Ranwell 1967; Aberle 1990; Mumford et al. 1990). Some introductions have been intentional (to stabilize shoreline erosion), while others have been accidental such as through the unloading of ship's ballast (Aberle 1990). *Spartina alterniflora* was introduced to San Francisco Bay, California in the mid-1970s during a marsh restoration project (Spicher and Josselyn 1985; Daehler and Strong 1994), but the plant is now widely recognized as an imposing invader. *Spartina alterniflora* threatens to transform the bay's open mud flats into vast monocultures of dense, 2 m-tall grass, modifying invertebrate communities and resulting in great loss of shorebird feeding areas (Callaway and Josselyn 1992). Attempts to control *Spartina* invasions around the world by mechanical disruption, shading, and herbicides have been costly and usually unsuccessful (Aberle 1990; Mumford et al. 1990). Very little is known about the impact of insect herbivores on cordgrass marshes (Adam 1990). The work of Bertness et al. (1987) and Bertness and Shumway (1992) suggests that insect herbivores may have great impact on *S. alterniflora's* sexual reproduction in its native Rhode Island habitat; however, the potential for biological control of introduced *S. alterniflora* by insect herbivores has yet to be explored. Biological control may have advantages over traditional control methods for *S. alterniflora* in terms of labor, monetary cost, and human health hazards (DeBach and Rosen 1991).

In San Francisco Bay, *S. alterniflora* is attacked by high densities of two sap-feeding insect herbivores. In this study we use field manipulations and greenhouse experiments to assess the impact of herbivory on the vegetative growth and seed production of introduced *S. alterniflora* in San Francisco Bay. The results are used to evaluate the potential for these herbivores to control *S. alterniflora's* invasion of San Francisco Bay.

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Materials and Methods

Study Organisms

Spartina alterniflora, smooth cordgrass, typically grows in extensive monocultures in its native habitat, the intertidal mud flats of the Atlantic and Gulf coasts of North America (Adam 1990). The plant can spread by both seed and vegetative fragments and is presently abundant at several sites in south San Francisco Bay. In recently colonized areas, *S. alterniflora* grows in circular patches separated by open mud. These circular patches consist of individual genetic clones (Daehler and Strong 1994). The two insect herbivores attacking *S. alterniflora* in San Francisco Bay are *Prokelisia marginata* Van Duzee (Homoptera), a plant hopper, and *Trigonotylus uhleri* Reuter (Miridae), a mirid bug. Both insects are *Spartina* specialists and are common herbivores of *S. alterniflora* on the Atlantic Coast of North America (Denno 1977; Strong and Stiling 1983; Denno 1985). In San Francisco Bay, these herbivores also feed on the native *Spartina foliosa*. *P. marginata* appears to be a native herbivore of *S. foliosa* on the Pacific Coast of North America (Wilson 1982). During three summers of censusing (1991–1993), *Prokelisia marginata* reached peak densities approaching 1,000 individuals per culm of *S. alterniflora* and consistently reached densities of 300 per culm by early fall (Daehler unpublished data). These densities are far higher than densities typically reported from *S. alterniflora's* native habitat (e.g., Denno et al. 1980; Strong and Stiling 1983). *Prokelisia marginata* completes three to four fairly discrete generations per season in San Francisco Bay, with increasing peak densities from June until November, when populations drop sharply until spring (Roderick 1987; Daehler unpublished data). *Trigonotylus uhleri* was not recorded to occur on the Pacific Coast of North America prior to our 1993 collection in San Francisco Bay (identified by T. J. Henry, Systematic Entomology Laboratory, United States Department of Agriculture). During the summer of 1993, *T. uhleri* reached densities as high as 10 individuals per mature culm of *S. alterniflora.*

Field Manipulation of Insect Densities

To evaluate the influence of herbivory on plant growth and reproductive output, insect herbivores were killed on individual clones of *S. alterniflora* in the field using a contact insecticide, 1:50 Safer Insecticidal Soap (Safer Inc., Newton, Massachusetts, USA). We tested for effects of this insecticide on the growth of *S. alterniflora* (see Effects of insecticide on plants, below). A total of 16 circular clones were used to evaluate the effects of herbivory on plant growth in the field. Clone sizes ranged from 1.5 m to 2.5 m in diameter, and each was separated from surrounding plants by 1–3 m of open mud. Half of the clones were randomly assigned to be sprayed with insecticide followed by a freshwater rinse. The remaining eight control clones were sprayed with only a freshwater rinse. Spraying was done weekly for 14 wk, beginning in early July and ending in mid October. During a 3-wk period beginning in late August, spraying was done twice per week, since a large cohort of winged adult *P. marginata* recolonized sprayed patches more rapidly during that time. To measure the effectiveness of insecticide spraying, herbivore densities were estimated on control and insecticide-sprayed plots on several dates, both just prior to spraying and midweek after spraying. Densities were estimated by counting all herbivores on five different stems of a clone. Counted stems were chosen randomly with the constraints that stems were approximately average height for the clone and could be counted without trampling the clone. Counts from at least four different control and sprayed clones were used to estimate herbivore densities during each census. This procedure proved to be very time consuming, especially on control clones, so counts could not be made every week.

Effect of Insecticide on Plants

Initial greenhouse trials had shown that long-term, repeated spraying of *S. alterniflora* with Safer Insecticidal Soap could cause etiolation of leaves under the following conditions: spraying during strong sunlight and high leaf temperature (above about 28°C, also not advised by the manufacturer); allowing residue to build up on leaves as a result of repeated spraying and drying. We took several steps to ensure a minimum effect of the insecticide on our field plants. To avoid strong sunlight and high leaf temperatures, we usually sprayed within 1 h of sunrise, and never more than 3 h past sunrise. After spraying with insecticide, we rinsed clones with fresh water to eliminate build-up of residue. Tides normally flooded the clones twice daily, removing any remaining residues from most leaves and washing away residue from the mud beneath clones.

We conducted experiments to test the effect of a similar treatment regime on greenhouse plant growth. In the first experiment, a total of 40 potted *S. alterniflora* seedlings of approximately uniform size were used. Half were randomly assigned to be sprayed weekly with insecticide followed by a freshwater rinse. The controls were rinsed with fresh water only. These plants were fertilized biweekly with a solution of Plantex 20-20-20 fertilizer. In the second experiment, seeds were germinated from

10 different clones from the field site and a pair of similar-size seedlings was chosen from each maternal clone. One seedling from each pair was randomly assigned to be sprayed with insecticide while the other was sprayed with water. These plants were fertilized twice per week with the same fertilizer solution as the first experiment. The experiments were carried out for 10 consecutive weeks, and during the last 3 wk plants were sprayed twice per week. At the end of the experiment, plants were harvested, dried to a constant mass at 70°C, and compared between treatments.

Vegetative Growth Rates in the Field

Prior to the first spraying in early July, five mid-sized stems (about 30 cm tall, hereafter referred to as juvenile stems) and 10 small shoots (about 15 cm tall, hereafter referred to as shoots) were marked on each clone using numbered flags. The height of each of these stems was measured weekly during the course of the experiment. Stem height is strongly correlated with dry mass of stems in *S. alterniflora* (Nixon and Oviatt 1973). Using stems collected from our study site, a logarithmic transformation of both height and dry mass yielded a correlation of $r = 0.983$ ($n = 51$, $p < 0.001$).

To compare vegetative growth rates between sprayed and control clones, we used a discrete measure (McGraw and Garbutt 1990) of relative growth rate (RGR),

$$RGR = (h_{t+1} - h_t)/h_t$$

where h_t is the height at time t and h_{t+1} is the height 1 wk later (e.g., Thomas and Bazzaz 1993). Because height is strongly correlated with biomass, this measure of growth is directly proportional to growth rate measured by change in biomass (Daehler unpublished results).

Lateral Spread in the Field

In early July, a 3-m-long wire was pressed in the mud as a tight semicircle around the edge of each circular clone. At that time, no shoots were outside the wire. The wire was held firmly in place with several stakes. In mid-October, we counted the number of new shoots outside the wire to quantify lateral spread.

Sexual Reproduction in the Field

At the conclusion of the field experiment in early November, all inflorescences from the 16 experimental clones were harvested just prior to natural loosening of the spikelets. The relative number of inflorescences (per m^2) were determined as a measure of allocation to flowering. All spikelets were then counted and the proportion of spikelets containing seed was used as a measure of seed production.

Greenhouse Herbivory Experiment

In mid July, *S. alterniflora* seedlings were potted with a mixture of 25% Bodega Bay mud and 75% Vermiculite (by volume) into 4 cm diameter × 15 cm deep growth tubes and placed into four trays. Each tray contained a total of 30 plants, with five individuals from each of six different maternal families. The position of each individual within a tray was randomized and plants were generously spaced to minimize edge effects. Three trays of plants were then inoculated with *P. marginata* and *T. uhleri* collected from the field (initial densities: approximately 5 *P. marginata* per plant and approximately 0.25 *T. uhleri* per plant). Insects were observed to move readily between plants within inoculated trays by hopping; insect densities were determined from biweekly counts. The fourth tray of 30 plants served as a herbivore-free control. Plants were grown on the same greenhouse bench and the position of trays was rotated biweekly to minimize lighting effects. To prevent colonization of the control plants by herbivores, the control tray was always separated from the infested plants by a 1.5 m-wide barrier of dead, dried *S. alterniflora* stems. This barrier was approximately the same height as the initial experimental plants and was highly effective. The occasional insect observed on control plants was immediately removed by hand. Biweekly, each tray was given 1 g of Plantex 20-20-20 fertilizer dissolved in water; growth tubes were kept saturated with fresh water. After 12 wk of herbivory, plant shoots and roots were dried to a constant mass at 70°C. Dry mass and number of shoots per plant were compared between herbivore treatment and control plants.

Statistics

Statistical analyses were performed using the SYSTAT system (Wilkinson 1990). Differences in growth rate between insecticide-treated and control clones in the field were tested using ANOVA with clone nested within treatment (insecticide versus control). Growth rates were treated as repeated measures (Sokal and Rohlf 1981; Neter et al. 1990). Treatment means were then compared for each measurement time using univariate F-tests corrected for multiple comparisons by a sequentially rejective Bonferroni procedure (Holm 1979). Separate ANOVAs were used for the measurements of juvenile stems and measurements of shoots, since the timing of growth was not directly comparable (juvenile stems reached maximum height much earlier than shoots). Growth rate measurements toward the end of the season could not be

TABLE 1. Effect of insecticide treatment on the growth of greenhouse *Spartina alterniflora* plants. Measurements were made on plant dry mass (g) and are given as ±1 standard deviation.

	Insecticide	Control	p-value
	Biweekly Fertilizer Addition		
Aboveground biomass	0.321 ± 0.078	0.341 ± 0.072	0.418[a]
Total plant biomass	0.772 ± 0.154	0.873 ± 0.234	0.115[a]
	Twice-weekly Fertilizer Addition		
Aboveground biomass	7.83 ± 5.84	8.61 ± 5.19	0.563[b]
Total plant biomass	10.74 ± 7.60	12.32 ± 7.34	0.351[b]

[a] Independent samples t-test between insecticide-sprayed and control (water sprayed) plants, n = 40.

[b] Paired samples t-test between pairs of sibling seedlings of the same initial size, one sibling sprayed with insecticide, the other sprayed with water, n = 20.

analyzed using the ANOVA because many zeros in the data violated the assumption of normality (although heteroscedasticity was not a problem). For these end-of-season measurements we used the nonparametric Mann-Whitney U statistic to compare mean growth rates of insecticide-treated and control clones (Daniel 1990). Lateral growth rate and relative number of inflorescences were compared between sprayed and control clones using t-tests assuming separate variances (Wilkinson 1990). The greenhouse herbivory experiment was analyzed with ANOVA using initial plant height as a covariate. Tray and family were treated as main effects. We then tested for significant differences among the trays using a Tukey test for multiple comparisons (Neter et al. 1990).

Results

Effect of Insecticide on Greenhouse Plants

For both greenhouse experiments, there were no significant differences between the insecticide-sprayed and control greenhouse plants in either aboveground plant biomass or total plant biomass (Table 1, t-tests), indicating that our spray treatments do not significantly affect the growth of *S. alterniflora*.

Impact of Insecticide on Herbivore Densities

Virtually all herbivores counted on insecticide-treated patches were immigrants from surrounding plants, since the insecticide proved extremely effective in killing insects at the time of spraying. Mid-week censuses showed that sprayed clones averaged herbivore densities that were 10–30% of controls. A full week after spraying, herbivore densities on insecticide-treated clones usually averaged less than 50% of those on control clones (Figs. 1 and 2). Throughout the experiment, the range of mean *P. marginata* densities on insecticide-treated plants a full week after insecticide treatment was 40–177 insects per stem, while control clones averaged 113–353 insects per stem.

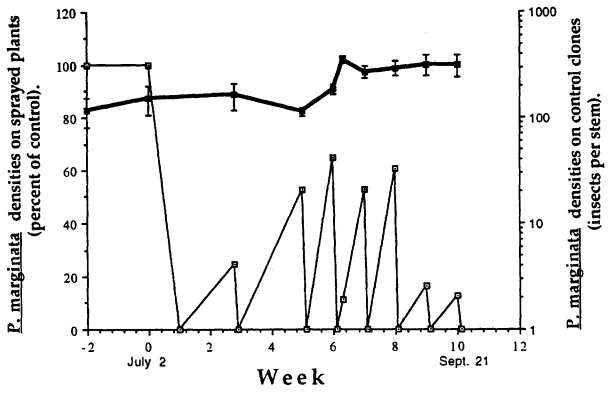

Fig. 1. Mean number of *Prokelisia marginata* per stem on control *Spartina alterniflora* plants during the course of the herbivore reduction experiment (thick line, right axis, log scale, error bars indicate 1 SE) and mean *P. marginata* densities on insecticide-treated plants, expressed as percent of control plants (left axis, thin line). Dates of insecticide treatment are indicated by zero *P. marginata* densities on the left axis. Insecticide-treated clones usually carried far less than half of the herbivore load of control clones. Insect censuses were terminated after September 21 (week 10); however, insecticide treatments continued through October (week 14).

Effects of Herbivory-Field Study

For growth measurements on juvenile stems, there was a significant difference between insecticide-treated and control clones only during the first week following spraying, with insecticide-treated clones having a more rapid growth rate (Fig.

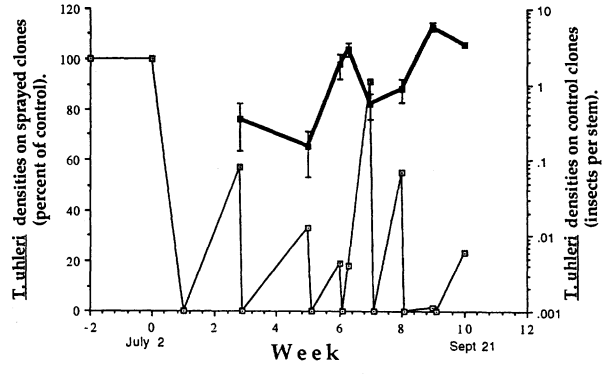

Fig. 2. Mean number of *Trigonotylus uhleri* per stem on control *Spartina alterniflora* plants during the course of the herbivore reduction experiment (thick line, right axis, log scale, error bars indicate 1 SE) and mean *T. uhleri* densities on insecticide treated plants, expressed as percent of control plants (left axis, thin line). Censuses of *T. uhleri* were not begun until week 3 and were terminated after week 10. Insecticide treatments were continued through October (week 14).

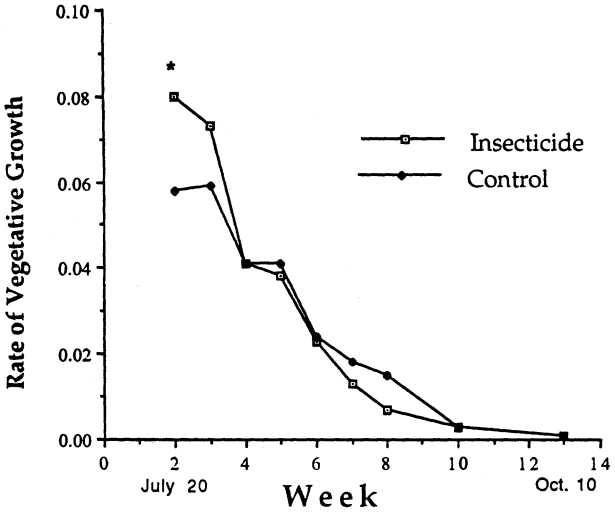

Fig. 3. Field vegetative growth rates (g g^{-1} wk^{-1}) measured from juvenile (initially about 30 cm tall) stems of *Spartina alterniflora* followed over summer on insecticide-treated (open squares) and control clones (solid diamonds). Asterisk indicates significant difference between insecticide-treated clones and controls (only on week 2), (Bonferroni test for multiple comparisons, $p < 0.05$). Growth rate declined through the summer and averaged near zero by week 10. Discrete growth rate was measured as (height at week x + 1 − height at week x)/(height at week x). This measure is strongly correlated with growth rates measured from dry mass.

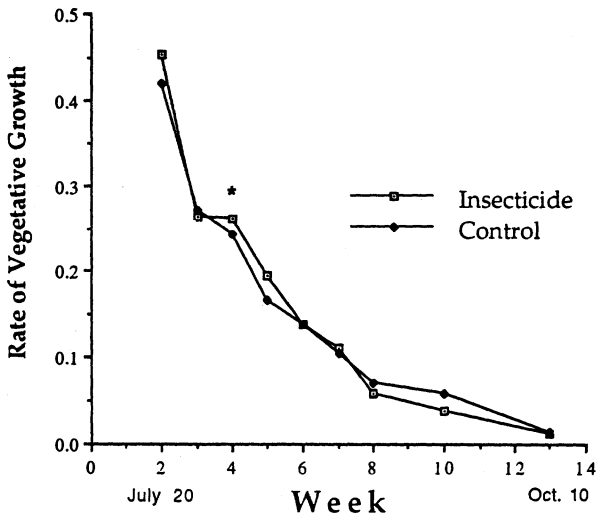

Fig. 4. Field vegetative growth rates (g g^{-1} wk^{-1}) measured from shoots (initially about 15 cm tall) of *Spartina alterniflora* followed over summer on insecticide-treated (open squares) and control clones (solid diamonds). Scale differs from Fig. 3. Asterisks indicate significant differences between insecticide-treated clones and controls (only on week 4) (Bonferroni test for multiple comparisons, $p < 0.05$). Growth rates approached zero by week 13. Discrete growth rate was measured as (height at week x + 1 − height at week x)/(height at week x). This measure is strongly correlated with growth rates measured from dry mass.

3). For growth measurements on shoots, there was a significant difference only after the second week of measurements, with shoots from insecticide-treated clones growing more rapidly (Fig. 4). Both juvenile stems and shoots showed a significant effect of time, decreasing in growth rate through the season; however, shoots also showed a significant interaction of time and clone ($p = 0.004$), suggesting that different clones showed different patterns of growth over time. There was no treatment × time interaction ($p = 0.441$). Insecticide-treated and control clones produced a similar number of inflorescences and both had equally low rates of seed set (Table 2). The rate of lateral spread was found to be positively correlated with clone area. This correlation was effectively removed by dividing the number of new shoots outside the marking wire by clone area. Using this relative measure, there was no difference between mean rate of spread of insecticide-treated and control clones (Table 2).

Effects of Herbivory, a Greenhouse Study

One week following inoculation of greenhouse plants, *P. marginata* densities averaged about 4 per plant (approximately 9 g^{-1} aboveground dry mass, compared to approximate field densities at the time of 15 g^{-1} plant dry mass). By week 6, greenhouse densities had increased to levels similar to those in the field, and by week 10, following emergence of a large second cohort of eggs, greenhouse plants averaged 40 *P. marginata* g^{-1} dry mass, while field plants only averaged 21 *P. marginata* g^{-1} dry mass. Densities of *T. uhleri* on greenhouse plants were similar to field densities throughout the experiment, averaging about 1 *T. uhleri* g^{-1} dry biomass.

In the greenhouse herbivore treatments, six out of 90 seedlings died, while none of the 30 control seedlings died. The seedlings that died were some of the smallest individuals at the start of the experiment (all less than 15 cm tall) and all dead

TABLE 2. Reproductive output and vegetative spread of *Spartina alterniflora* clones in the field with natural herbivory (control) and reduced herbivory (insecticide). p-values are given for t-tests assuming unequal variances. n = 8 clones per treatment.

	Insecticide	Control	p-value
Reproductive output			
Clones not flowering	1	1	
Inflorescences m^{-2}	8.2 ± 7.3	14.4 ± 13.6	0.28
Percent seedset	0.32 ± 0.18	0.44 ± 0.31	0.76
Vegetative spread			
New sprout m^{-1}	6.8 ± 3.4	10.7 ± 6.4	0.16

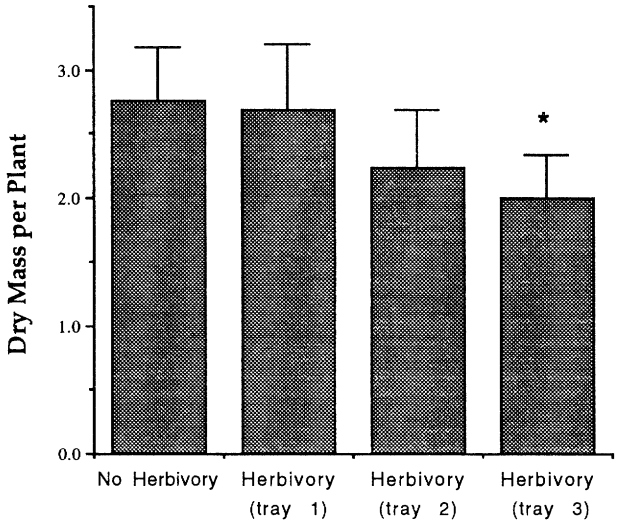

Fig. 5. Mean dry mass (g) of greenhouse plants without herbivory and greenhouse plants from three different trays subjected to herbivory by *Prokelisia marginata* and *Trigonotylus uhleri* for 12 wk. Error bars indicate 95% confidence intervals (Tukey HSD method) and the asterisks indicate a significant difference between herbivory and no herbivory plants ($p < 0.05$). Each replicate tray was inoculated with similar numbers of herbivores. Herbivore densities were similar to those observed in the field.

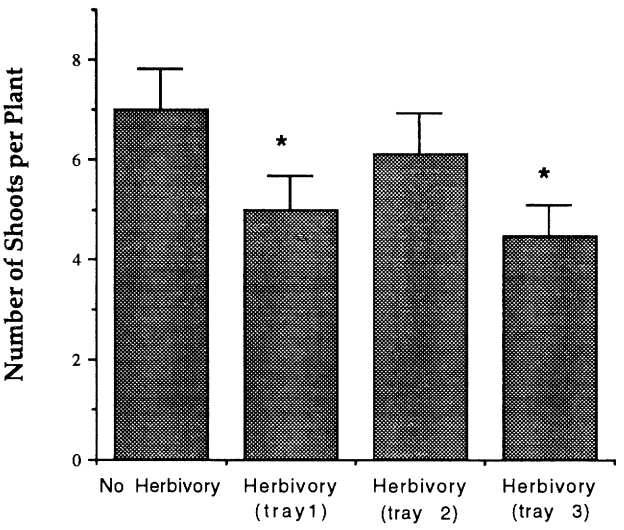

Fig. 6. Mean number of shoots on greenhouse plants without herbivory and greenhouse plants from three different trays subjected to herbivory by *Prokelisia marginata* and *Trigonotylus uhleri* for 12 wk. Error bars indicate 95% confidence intervals (Tukey HSD method) and the asterisks indicate a significant difference between herbivory and no herbivory plants ($p < 0.05$). Each replicate tray was inoculated with similar numbers of herbivores. Herbivore densities were similar to those observed in the field.

seedlings had grown less than 2 cm before dying. Dead plants were excluded from the statistical analyses.

Because aboveground biomass was found to be strongly correlated with total biomass ($r = 0.951$), an ANOVA was run only on total plant biomass, transformed logarithmically to fulfill assumptions of normality and homogeneity of variance. There was a significant overall effect of tray ($p = 0.033$); however, comparison of treatment means between the no-herbivory tray and herbivory trays shows that only one of the herbivore treatment trays had significantly lower mean plant biomass than the control tray (Fig. 5). There was also a significant family effect for total plant biomass ($p < 0.001$), but no interaction between family and treatment ($p = 0.33$).

In testing the effect of herbivory on total number of shoots, the data were log-transformed to fulfill the major assumptions of ANOVA. There was a significant effect of tray ($p = 0.043$). Examination of the means between the control tray and the herbivory trays showed that two herbivory trays averaged significantly fewer shoots than the control tray, but the third herbivory tray did not differ from the control (Fig. 6). There was a significant effect of family ($p = 0.001$) on shoot number and there was a significant family × tray interaction ($p = 0.004$). This interaction became nonsignificant when one family that had shown an increase in mean number of shoots in the herbivore treatment was excluded from the analysis.

Discussion

Herbivory and Vegetative Growth

Our manipulations of herbivore densities in the field suggest that the extraordinarily high *P. marginata* and *T. uhleri* densities have little consistent effect on vegetative growth rates of *S. alterniflora* in San Francisco Bay. The analyses based on shoots and juvenile stems had the power to detect approximately 12% and 20% differences, respectively, between mean growth rates of insecticide-treated and control plant during a given week of growth (at a family-wide significance level of 0.05). Greater differences in growth rates might have been observed in the field had we been able to exterminate continuously all herbivores on the insecticide-treatment clones; however, given the marginal differences observed in the greenhouse where control plants were virtually herbivore-free and environmental variance was minimized, we doubt if a large difference would have been found had all herbivores been exterminated in the field. The greenhouse study had the power to detect approximately a 25% difference in dry mass between herbivore and herbivore-free plants (at a significance level of 0.05).

Our study lasted for only one growing season

and there is a possibility that long-term, chronic herbivory by these sap-feeding insects may be slowing the vegetative spread of *S. alterniflora.* This hypothesis is not supported by a comparison of rates of lateral spread in San Francisco Bay, where plants suffer herbivory by *P. marginata* and *T. uhleri,* and in Willapa Bay, Washington, where no insect herbivores attack *S. alterniflora.* At both invasion sites the rates of lateral spread are similar, ranging from 0.5 m yr^{-1} to 1 m yr^{-1} (Sayce 1988; Daehler unpublished data).

In other studies of the effects of sap-feeding insects on plants, highly significant reductions in plant growth or survival have been observed, usually within 8 wk of the herbivore manipulations (e.g., Kantack and Dahms 1957; Mittler and Sylvester 1961; Mallott and Davy 1978; Kamm 1979; Wood et al. 1985; Reed and Semtner 1992; Deberardinis et al. 1994). In most of these studies the plants were perennials, and the plants were always of agricultural importance. Not surprisingly, these studies document large effects of sap-feeders because the herbivores studied were recognized a priori as causing major economic losses in the crops.

On the other hand, in a noncrop plant (*Solidago altissima*), aphid feeding had no detectible effect on plant growth (Meyer 1993). More studies on sap-feeders of non-crop plants are needed to evaluate the range of impacts that sap-feeders might have on plant vegetative growth in nature. We suspect a bias toward reporting strong effects of herbivores on host plants. The large body of literature reporting major effects of sap-feeders on agricultural crops may not be relevant to natural systems given recent evidence suggesting wild plants may be more tolerant to herbivory than their domesticated crop relatives (Welter and Steggall 1993).

Herbivory and Plant Mortality

In the greenhouse study, herbivory did apparently kill a few of the smallest seedlings. The impact of herbivory on seedlings was expected to be higher than on established plants because seedlings lack the belowground reserves of adult clones (Harper 1977). On San Francisco Bay mud flats, we have never found evidence that insect herbivory alone causes death of seedlings, established clones, or even individual tillers. In the field, many seedlings grow alone on open mud and have virtually no herbivores. Interestingly, a potentially important cause of shoot mortality in the field is herbivory by rodents. Tracks and scats from unidentified rodents (either the muskrat, *Ondatra zibethica,* or black rat, *Rattus rattus,* both introduced) were often observed in the mud beneath *S. alterniflora* where young shoots had been freshly gnawed near their bases. Attacks were patchy but thorough, with 20 or more young shoots being gnawed during single feeding bouts. During the course of the growing season, but primarily toward the end of the season, 19% of all our marked shoots were chewed near the base by rodents. These shoots always died (and were excluded from analysis after being chewed). But *S. alterniflora* is known to tolerate grazing and mowing, and in some cases, mowing plants as a control measure may even increase plant growth rate, stimulating the production of additional new shoots (Aberle 1990; M. Taylor personal communication). Van der Meijden et al. (1988) have suggested that a high root:shoot ratio may be an indication of ability to tolerate high herbivory, since these plants may have excellent regrowth capacity. The root:shoot ratio of *S. alterniflora* typically ranges from 1 to 2 (Smart 1986), comparable to that of *Senecio,* a plant cited as herbivory tolerant by van der Meijden et al. (1988).

Herbivory and Seed Production

Spartina alterniflora clones vary greatly in seed production in San Francisco Bay. Most clones set very few seeds (Daehler and Strong 1994). Reducing herbivory with insecticide treatments did not increase seed set in the present study. Previous work in *S. alterniflora's* native range showed that herbivores damaged many ovules and anthers, causing reduced seed set (Bertness and Shumway 1992). The primary herbivore causing damage in that study was a grasshopper, *Conocephalus spartinae,* which is not present in San Francisco Bay. Sap-feeding insects have been shown to reduce seed set in some grasses, causing silvertop-white inflorescences with withered stems (Starks and Thurston 1962; Kamm 1979). Silvertop culms usually set no seed. We have never observed the symptoms of silvertop on *S. alterniflora,* although seed set is often very low independently of herbivory.

Other evidence that suggests sap-feeding insects in San Francisco Bay have very little effect on seed set comes from a comparative study of seed set in Willapa Bay, Washington (USA) (Daehler and Strong 1994). *Spartina alterniflora* introduced to Willapa Bay has spread in the absence of all insect herbivores, yet clones in Willapa Bay have a similar frequency distribution of seed set to those in San Francisco Bay, with most clones setting very few seeds. When seed set is low due to factors that may be intrinsic to the plant (like seed abortion), the relative effects of even heavy herbivory on seed set may be minor (e.g., Traveset 1994). Seed set in this primarily outcrossing invader may be limited by viable pollen, or abortion of fertilized or unfertilized ovules due to recessive lethal alleles (Weins et al. 1987) rather than herbivory.

Potential for Herbivore Control of *S. alterniflora*

The growth of the herbivore populations is seasonal and distinctly correlated with the aboveground growth of *S. alterniflora*. Sparse herbivore populations in May and June increase to very dense populations in September and October, which then drop rapidly during November (Roderick 1987; Daehler unpublished data). The population crash of herbivores in November is probably the result of mortality due to seasonal changes in plant nitrogen. Nitrogen content in all aboveground parts of *S. alterniflora* drops rapidly in late fall as mature stems die (Squiers and Good 1974). Seasonal changes in plant nitrogen occur independent of herbivory, and the accompanying herbivore population crashes suggesting this particular set of species in the *S. alterniflora* food web in San Francisco Bay is primarily donor-controlled (Strong 1992); the primary producer controls production of herbivores, carnivores, and detritivores, with consumers having little if any reciprocal effects upon levels of their resource species. The parasitoid *Anagrus delicatus* kills some eggs of *P. marginata,* but the mortality is low and inversely density-dependent (Stiling and Strong 1982; Strong 1989; Cronin and Strong 1990), so the top-down effects of natural enemies on *P. marginata* are minimal in San Francisco Bay.

One possible reason why high herbivore densities have so little effect on *S. alterniflora* is that the plant suffers no interspecific competition. It grows uncrowded, invading rich, open mud. Under these conditions, stresses due to light and nitrogen limitations are reduced in comparison with established stands. Herbivory can be most effective in damaging plants growing under stressed conditions like high plant density (Lee and Bazzaz 1980; Dirzo 1984). Often, herbivory can regulate a plant population indirectly by altering competitive hierarchies among plant species, making the attacked species more vulnerable to interspecific competition (Crawley 1983; Cottam et al. 1986; Louda et al. 1990). In the case of the monospecific *S. alterniflora* community of the lower intertidal, there are no plant competitive hierarchies for herbivores to alter, possibly making herbivore regulation of this plant especially difficult. In some cases, nitrogen supplements have been necessary for successful herbivore control of an introduced plant growing in monospecific stands (Thomas and Room 1986). In its native environment, *S. alterniflora* supplemented with nitrogen fertilizer did have higher herbivore densities; however, fertilized plants also had increased standing biomass (Vince et al. 1981), the opposite of what would be expected if herbivory were regulating plant biomass.

From both the field and greenhouse results of this study, it appears unlikely that herbivory by high densities of the sap-feeding insects *P. marginata* and *T. uhleri* alone will be able to control the invasion of *S. alterniflora* in San Francisco Bay. There is no evidence that feeding by these insects alone has an important effect on vegetative growth or seed production in the field. Other insects native to the Atlantic Coast of North America could act more effectively as biocontrol agents, especially if introduced without parasitoids. For example, insects with stem-boring larvae that kill meristems, like *Chilo plejadellus* (Lepidoptera), and inflorescence-killing midges like *Calamomyia alerniflorae* (Strong et al. 1984) would seem to have greater potential for controlling *S. alterniflora*; however, their introductions would require extensive, prerelease screening to ensure that no other plant species were attacked.

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