Mechanisms of Expansion for an Introduced Species of Cordgrass, *Spartina densiflora,* in Humboldt Bay, California

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ABSTRACT: The dominant plant in Humboldt Bay salt marshes is *Spartina densiflora*, a species of cordgrass apparently introduced from South America. At several salt marshes and restoration sites around Humboldt Bay, distribution of this plant has increased significantly. We investigated the relative contributions of vegetative tiller production and seed germination to the establishment and expansion of *S. densiflora*. Lateral spread of plants surrounded by competitors were compared to areas without competing plant species. Plants growing in areas without competitors had significantly higher rates of vegetative expansion ($p < 0.0001$). Viable seed production, germination rates, seedling survivorship, and growth of adult plants were measured in six salinity treatments. Approximately $1,977 \pm 80$ viable seeds are produced per plant (0.25–0.5 m²). The number of germinating seeds was inversely related to increases in salinity. Salinity treatments between 19‰ and 35‰ produced significantly lower germination rates than salinities of 0–18‰ ($p < 0.0001$). Seedling survivorship was 50% at ≤4‰ and 8–14% at ≥11‰. Lateral expansion of adult, greenhouse-grown plants occurred in all salinity treatments, with modest decreases in the highest salinity treatments ($p < 0.05$). Our findings indicate that *S. densiflora* expands primarily by vegetative expansion, and lateral tillers are produced by throughout the year. *Spartina densiflora* produces prolific amounts of seed, but recruitment in mature salt marshes may be limited by competitors and higher salinities. At restoration sites, planting of native species such as *Salicornia virginica, Distichlis spicata,* or *Jaumea carnosa* may prevent monospecific stands of *S. densiflora* from developing.

Introduction

Humboldt Bay salt marshes contain an assemblage of plant species found in neither Pacific northwest or southern California salt marshes (MacDonald and Barbour 1974; United States Army Corps of Engineers 1976). In addition to representing a transitional area for salt marsh flora, Humboldt Bay is distinct from other west coast salt marshes because of the presence of *Spartina densiflora,* a species native to South America (Spicher 1984).

Dense-flowering cordgrass, *S. densiflora,* occupies an enigmatic position in the floras of California. It was long thought to be an ecotype of a native cordgrass, *Spartina foliosa* (Saint-Yves 1932; Mobberley 1956; MacDonald 1977) until specimens from Humboldt Bay were transplanted to San Francisco Bay in 1977 (Spicher and Josselyn 1985). Numerous phenological and ecological differences between *S. foliosa* and Humboldt Bay cordgrass immediately became apparent (Spicher 1984). Using herbarium samples, Spicher (1984) concluded that cordgrass in Humboldt Bay was probably *Spartina*

densiflora Brong. forma *acuta* St. Y., a species native to South America. He further speculated that *S. densiflora* probably had been introduced by the lumber trade that flourished in the late 1800s between northern California and Chile. P. Faber (personal communication, California Native Plant Society) and B. Crampton (personal communication, University of California, Davis) verified his identification with specimens of *S. densiflora* collected in Chile. Since the identification of cordgrass in Humboldt Bay, there have been no reports of *S. foliosa* north of Bodega Bay, California (Spicher and Josselyn 1985).

Native species of *Spartina* have been used as stabilizers of exposed mudflats or dredged material in marsh reclamation projects (Woodhouse et al. 1972, 1976; United States Army Corps of Engineers 1976). However, interest in marsh restoration as a mitigation measure has resulted in a number of introductions of non-natives into estuaries worldwide: *Spartina patens* in Suislaw Bay, Oregon (Frenkel and Boss 1988); *S. densiflora* and *Spartina alterniflora* in San Francisco Bay, California (Spicher and Josselyn 1985; Callaway 1991); and *Spartina anglica* in England, Europe, China, and New Zealand (Lee and Partridge 1983; Gray et al. 1990; Scholten and Rozema 1990). Species of *Spartina* can be aggressive and bothersome invaders of adjacent ma-

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rine mudflats (Josselyn and Buchholz 1984; Callaway 1991; Thompson 1991). Monospecific stands of introduced *Spartina* may result, often altering assemblages of native plants and invertebrates (Frenkel and Boss 1988). Declines in shorebird populations are also possible (Goss-Custard and Moser 1988).

In Humboldt Bay, *S. densiflora* grows abundantly and contributes significantly to the primary productivity of the estuarine ecosystem (Rogers 1981). *S. densiflora* grows in all 393 ha of salt marsh habitat existing within Humboldt Bay. *S. densiflora* is distributed primarily between 6.2 and 7.3 MLLW, but can occur as low as 5.9 and as high as 7.9 MLLW (Eicher 1987). In similar tidal elevations around Humboldt Bay, percent cover of *S. densiflora* is between 30% and 100% (Eicher 1987). At one site, which is less disturbed, cover was approximately 30% and individual clumps of *S. densiflora* were smaller (Eicher 1987). Monospecific stands generally occur at restoration sites and in disturbed salt marshes.

Even though *S. densiflora* is found throughout Humboldt Bay, there is concern that its cover and range are increasing. Approximately five marsh restoration sites within the bay have been accompanied by the rapid spread of *S. densiflora* over a significant elevational gradient (Claycomb 1983; personal observation). Also, in San Francisco Bay, *S. densiflora* recently colonized Point Pinole, presumably by seed from Corte Madera marsh where *S. densiflora* has been growing since 1977 (D. Strong, personal communication, University of California, Davis). For those who wish to understand and carry out marsh restoration activities, the presence of *S. densiflora* in Humboldt Bay presents significant challenges. *S. densiflora* is clearly an exotic but has spread to such an extent that eradication is impossible and probably undesirable. However, control may be possible in salt marshes where *S. densiflora* has recently invaded or where it is less widespread.

Properties enabling *Spartina densiflora* to be successful in Pacific coast salt marshes are poorly understood. Barnhart et al. (1992) speculated that establishment and expansion of *S. densiflora* may involve both vegetative tiller production and seed germination over a wide range of salinities. The relative contribution of these mechanisms to the expansion of *S. densiflora* in Humboldt Bay is not known.

The purpose of this investigation was to clarify the following life-history components for *S. densiflora*: to measure the rate of vegetative expansion for plants located in areas without competitors compared to those surrounded by native competitors: to determine the tolerances of seeds, seedlings, and vegetative tillers to a range of salinities potentially occurring in salt marshes: and to infer the relative contribution of seeds and vegetative tillers to the establishment and expansion of *S. densiflora*. If *S. densiflora* is able to withstand a wide range of salinities, reproduce successfully through seed production while also expanding laterally, *S. densiflora* could become more prevalent within Humboldt Bay or other Pacific coast salt marshes.

Methods

FIELD EXPERIMENTS

Study Site

Field experiments and plant collections were conducted at two sites in Humboldt Bay California, also known as Arcata or North Bay. All measurements of vegetative expansion occurred at the west side of the bay at Vance Street, north of the Somoa Bridge (Fig. 1). Seed and plant collections were made at that site and on the north side of the bay at Arcata Marsh (Fig. 1).

The salt marsh proper is dissected by tidal creeks and predominated by *Salicornia virginica* and *S. densiflora*. Other common salt marsh species include *Distichlis spicata*, *Jaumea carnosa*, and *Limonium californicum*.

Vegetative Expansion in the Salt Marshes of Humboldt Bay

We measured vegetative expansion for plants surrounded by potential interspecific competitors in undisturbed marshes and for isolated plants not surrounded by competitors. To measure expansion in the presence of competitors, undisturbed areas were chosen which did not have appreciable amounts of wrack deposition and which contained several native salt marsh species. To measure expansion without competitors present, we chose patches of *S. densiflora* surrounded by unvegetated salt marsh soil. These isolated patches of *S. densiflora* naturally occur as a result of wrack deposition. All areas selected for measurements of vegetative expansion did not differ significantly in elevation.

A total of 39 tussocks of *S. densiflora* were selected with the capacity to expand laterally by tillers. Plants in monospecific stands of *S. densiflora* were not used since vegetative expansion under such conditions is virtually impossible to discern. Plants surrounded by competitors were at least 25 cm away from conspecifics but adjacent to other salt marsh species (e.g., *Salicornia virginica*, *Distichlis spicata*, *Jaumea carnosa*, and *Limonium californicum*). Plants without surrounding competitors were at least 25 cm from any salt marsh species.

In February 1992, 24 plants surrounded by competitors (basal area of *S. densiflora* 0.2–0.5 m^2) were
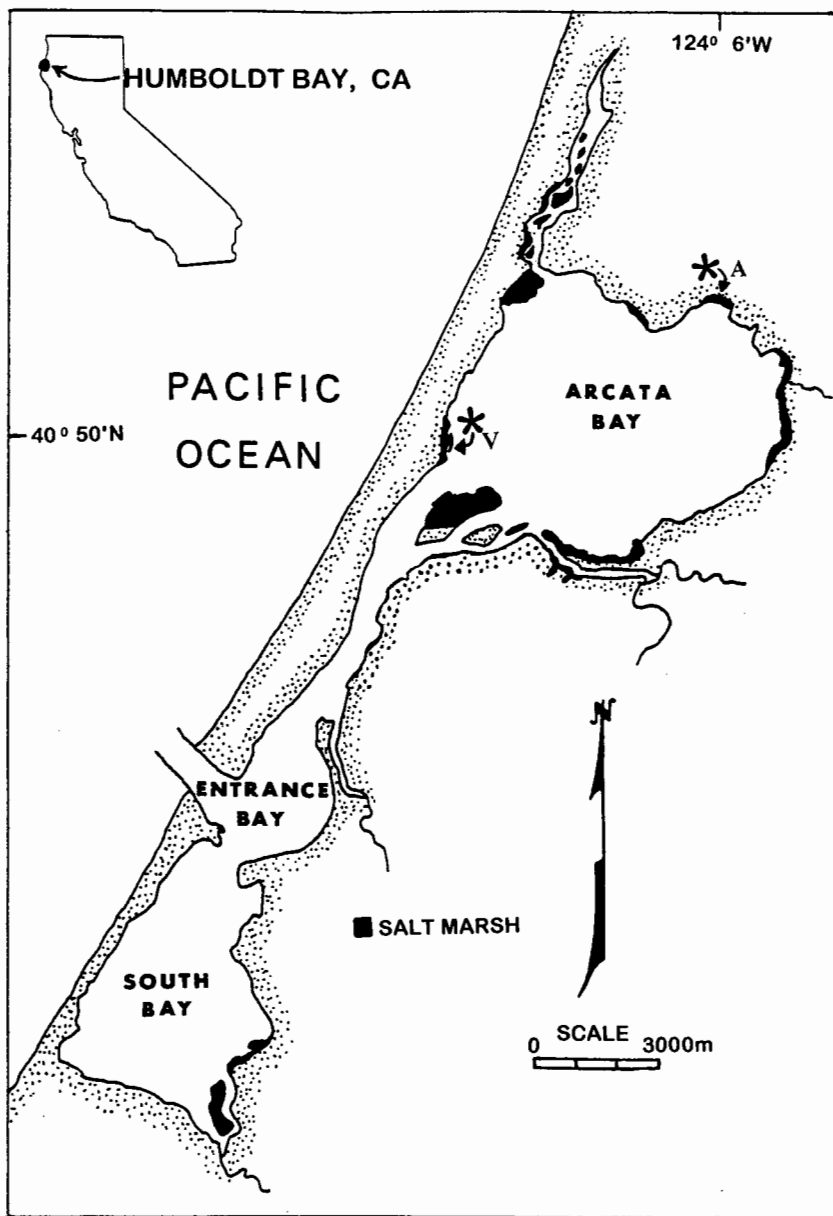
Fig. 1.   Humboldt Bay, California. An asterisk with the subscript V denotes the Vance Street site which served as the primary field sampling site and where *Spartina densiflora* seed was collected. An asterisk with the subscript A represents the Arcata Marsh, an area where additional *S. densiflora* seed was collected. Map modified, Barnhart et al. (1992).

marked with wooden stakes. An additional 15 plants not surrounded by potential competitors (basal area 0.15–0.45 m^2) were marked. The number of flowering culms, new lateral tillers, height, and basal circumference of *S. densiflora* were measured every 3 mo starting in February 1992 and ending in February 1993.

We monitored soil salinities at the study area every 3 mo from February 1992 to February 1993. Approximately 125 cm^3 of soil were placed in a plastic bag (n = 25). We measured the salinity of

centrifuged, interstitial water (4,000 rpm for 2 minutes) using a hand-held refractometer. Soil salinity also was measured at five locations during 1 d in February 1995 following a period of heavy rain.

Seed Production and Viability

Numbers of inflorescences were counted for all the marked plants (n = 39). Potential seed production was determined by counting the number of spikelets and developed seeds on 22 inflorescences from each of the 24 plants surrounded by

competitors. Inflorescences were haphazardly collected from plants ranging in basal area from 0.25 m^2 to 0.5 m^2. This size range represents most mature *S. densiflora* in Humboldt Bay salt marshes. Seed viability tests were conducted using tetrazolium chloride on four seeds from 125 arbitrarily chosen inflorescences (Dafni 1992).

GREENHOUSE EXPERIMENTS

Seed Germination Under Different Salinity Regimes

Salinity tolerances of *S. densiflora* propagules were examined by germinating seeds across a range of salinities and in distilled water. To determine if storage time affected germination and if seeds required ripening, two experiments were initiated with seed stored for different lengths of time. Germination experiment 1 was started in January 1992 with seeds which had been stored dry at 0°C for 18 wk (128 d). Germination experiment 2 was begun in April 1992 with seeds stored dry at 0°C for 31 wk (217 d). Salinity treatments of 0‰, 4‰, 11‰, 18‰, 27‰, and 35‰ ± 1‰ were created using a dilution series of filtered, UV-sterilized seawater. Within each treatment, five petri dishes were filled with 30 ml solution at the appropriate salinity. Twenty seeds were arranged on filter paper in an inverted petri dish. Petri dishes were covered to prevent evaporation and were placed in a greenhouse under a 12:12 hour light:dark cycle.

Growth and Morphology of Seedlings in Six Salinity Regimes

Germinated seeds were removed from salinity treatments and planted in perlite. After 1 mo the seedlings were transplanted to pots containing 100 ml steer manure and 1 l standard potting soil. Seedlings were watered with the same salinity solutions in which germination had occurred (0‰, 4‰, 11‰, 18‰, 27‰, 35‰ ± 1‰). Seedling survivorship, leaf length (measured from the base of the shoot to the tip of the leaf (cm)), and secondary tillering were recorded each month.

Adult Plant Growth and Morphology Under Different Salinity Regimes

To examine the rate of vegetative expansion in a range of salinities, five adult *S. densiflora* plants were dug from arbitrary areas within the salt marsh at the Vance Street site and transplanted into 66 pots. The plants were randomly assigned to six treatment groups: 0‰, 4‰, 11‰, 18‰, 27‰, and 35‰. Each group was watered three times a week with 300 ml of the appropriate salinity solution. Soil salinity was measured each month and watering regimes were adjusted to keep soil salinities within the appropriate range (i.e., ± 1‰). Height measurements and the number of dead culms, live culms, and new tillers were recorded monthly.

STATISTICAL ANALYSES

Results were analyzed using the following statistical packages and analyses: Minitab was used for Mann-Whitney U and Chi square analyses (Ryan et al. 1984); SAS software for ANOVA and two-way ANOVA (SAS Institute, Inc. 1985), and NCSS software for MANOVA (Heinz 1992). Means are reported with standard deviations unless otherwise noted.

Results

FIELD EXPERIMENTS

Vegetative Expansion in Salt Marshes

Increase in basal circumference over 1 yr was significantly higher among plants in areas without competitors than among plants surrounded by competitors (Mann-Whitney U, p < 0.0001). Change in basal circumference of plants surrounded by competitors (n = 24) ranged between −0.6 m yr^{-1} and 0.26 m yr^{-1}, with a median of 0.09 m yr^{-1}. Basal circumference among plants in naturally occurring bare areas (n = 15) ranged from 0.05 m yr^{-1} to 0.56 m yr^{-1}, with a median of 0.23 m yr^{-1}.

To visualize increases in basal area relative to the initial size of the plant, we transformed basal circumference into percent increase in basal area over 1 yr. Percent increase in basal area of plants surrounded by competitors ranged between −19% and 34%, with a median of 14.5%. Percent increase in basal area among plants in naturally occurring bare areas was significantly higher and ranged from 0% to 1745%, with a median of 234% (Mann-Whitney U, p < 0.0001).

Soil salinities ranged from 29.7 ± 2.2‰ in February 1992 to 37.9 ± 2.7‰ in August 1992. Soil salinity can decrease for brief periods after heavy rains. In February 1995, we measured soil salinities of 19.4‰ ± 1.7‰.

Lateral tiller production over 1 yr averaged 55.3 ± 19.3 in plants surrounded by competitors. In bare areas, an average of 44.2 ± 18.9 tillers were produced over 1 yr. These means were not significantly different (Mann-Whitney U; p > 0.05). Plants with competitors shed more culms (17 ± 9.9) than plants in bare areas (6.3 ± 2.5; Mann-Whitney U; p < 0.0001).

Seed Production and Viability

The number of inflorescences produced by each marked plant (n = 39) was counted in August 1992. *S. densiflora* surrounded by competitors produced substantially more inflorescences than

TABLE 1. Estimated seed production of *Spartina densiflora* at Humboldt Bay, California. Inflorescences (n = 22) were collected in September 1992 from 24 marked plants ranging in size from 0.25 m² to 0.5 m² and surrounded by competitors. Numbers of undeveloped or shriveled seeds were compared to the number of developed seeds per spikelet. To test viability, four seeds from 125 inflorescences were exposed to tetrazolium chloride stains.

Mean Number of Inflorescences per Plant (n = 24)	Mean Number of Spikes per Inflorescence (n = 22)	Mean Number of Spikelets per Spike	Percent Developed Seeds per Spikelet
28.7 ± 16	9.05 ± 2.2	13.5 ± 3.3	72 ± 3

Total number of developed seeds per plant = 2,512 ± 105
Total number of viable seeds per plant = 1,977 ± 80

plants surrounded by unvegetated areas, free of competitors (28.7 ± 16 inflorescences per plant versus 2.8 ± 4 inflorescences per plant; Mann-Whitney U, p < 0.0001).

Mature inflorescences of *S. densiflora* collected from plants surrounded by competitors had an average of 122 ± 15 spikelets produced by each inflorescence (n = 22). Each spikelet has the potential to produce one viable seed, and 72% ± 3% of the spikelets contained developed seed. We estimated the average number of developed seeds per inflorescence and approximately 2,512 ± 105 developed seeds were produced for each plant ranging between 0.25 m² and 0.5 m² in size (Table 1). Viability tests on 500 randomly chosen seeds revealed that approximately 78.7% ± 3.2% seeds were viable for a total 1,977 ± 80 viable seeds per plant.

GREENHOUSE EXPERIMENTS

Seed Germination Under Laboratory Conditions

In both germination experiments 1 and 2, the number of germinated seeds was inversely proportional to increases in salinity (Fig. 2). A salinity treatment of 35‰ produced a significantly lower germination rate than distilled water in both germination experiments.

Seeds stored at 0°C for 128 d germinated best in salinity treatments of 0‰, 4‰, and 11‰ (ANOVA, p < 0.0001). A Ryan test for multiple comparisons (SAS Institute, Inc. 1985) showed that treatments of 18‰, 27‰, and 35‰ resulted in significantly fewer germinated seeds than salinities of 0‰, 4‰, and 11‰. Treatments of 27‰ and 35‰ produced significantly fewer germinated seeds than 18‰ (p < 0.0001). The lowest number of seeds germinated in undiluted seawater, 35‰.

Seeds stored at 0°C for 217 d had slightly different germination rates than those in experiment 1. The lowest number of germinated seeds still occurred in seawater, 35‰. However, more seeds germinated in higher salinities (e.g., 27‰). Ger-
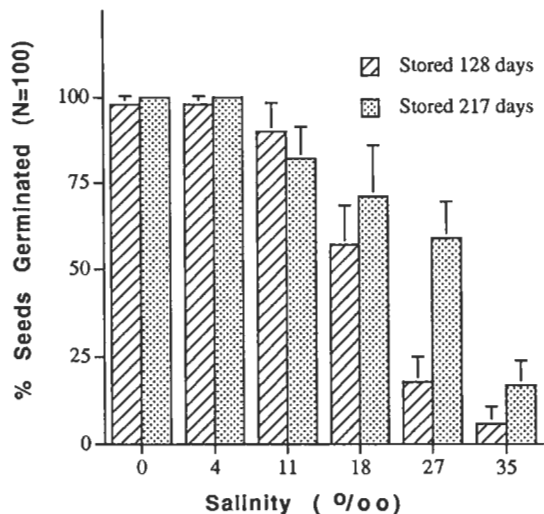

Fig. 2. Percentage of germinated seeds (n = 100) over six salinity treatments in germination experiments 1 and 2. Seed stored for 128 d were used in germination experiment 1. Seed stored for 217 d were used in germination experiment 2. Seed were collected from two sites in northern Humboldt Bay in October 1991.

mination rates in 27‰ were still significantly lower than at 4‰. The number of seeds germinated in treatments of 35‰ were significantly lower than all other salinities (ANOVA, p < 0.0001). A longer storage time (217 d) resulted in significantly higher germination rates when compared to storage time of 128 d (two-way ANOVA; p < 0.0001); also more seeds germinated in the higher salinities (Fig. 3).

Growth and Morphology of Seedlings in Different Salinity Regimes

After 6 mo, height of the seedlings was greater in lower salinity treatments: 0‰, 4‰, 11‰, 18‰, and 27‰ than in undiluted seawater, 35‰ (Fig. 4). Only seedlings grown in ≤27‰ produced secondary tillers. Leaf width was 3 mm for seedlings grown in ≤27‰, while leaf width was 2 mm for seedlings grown in 35‰.

Seedling survivorship was inversely related to increases in salinity (Table 2). Approximately 50% of the seedlings survived in salinities of 0‰ and 4‰. Approximately 10% of the seedlings in salinities ≥11‰ survived. Only one seedling survived in undiluted seawater, approximately 6% of the seedlings planted. A chi square test revealed that there was a highly significant inverse relationship between seedling survivorship and increased salinities (p < 0.0001).

Signs of salinity stress were common in salinity treatments ≥27‰. Initial culms appeared twisted and tightly rolled. Chlorosis appeared shortly after
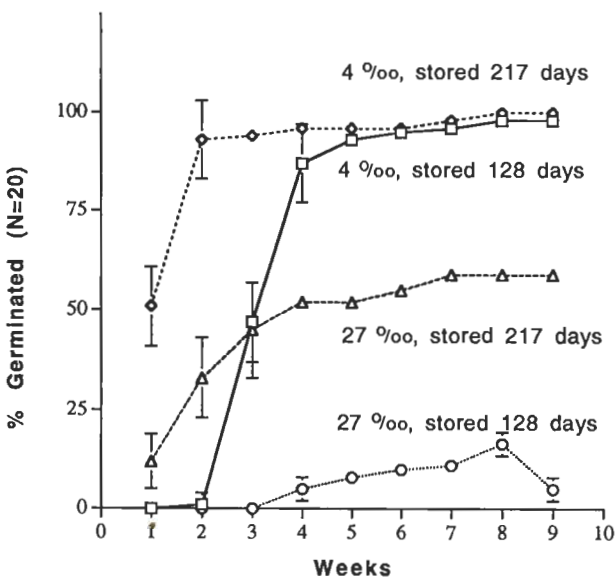
Fig. 3.   Percentage of seeds germinating over a period of 9 wk. Salinity treatments were 4‰ and 27‰ with seeds stored for 128 d for germination experiment 1 (I) and 217 d for germination experiment 2 (II) at 0°C.

elongation of the culm and necrosis occurred about 1 wk later.

Mature Plant Growth and Morphology Under Different Salinity Regimes

Mature *S. densiflora* growth was measured by combining the change in height, culm maintenance and tiller production over 8 mo. Plants grown in greenhouse conditions showed decreases in growth as salinities increased (MANOVA, p < 0.0001). Pairwise comparisons using Hotelling's T² and corrected for 30 multiple comparisons (Heinz

TABLE 2. Number of seedlings surviving and percent survivorship after 6 mo in each salinity treatment group. There is a significant relationship between salinity treatments and the number of seedlings surviving ($\chi^2 = 61.5$, df = 5, p < 0.0001).

Salinity (± 1 ‰)	Seedlings Planted	Number Surviving	Percent
0	70	35	50
4	70	33	47
11	70	10	14
18	60	5	8
26	55	6	11
35	17	1	6

1992) indicated that salinities of 0‰, 4‰, and 11‰ greater overall growth than salinities of 18‰, 27‰, and 35‰.

Univariate t tests at the 0.05 level indicated that change in height accounted for the overall significance in growth for adult plants (Fig. 5). The greatest increases in height were for plants treated with water at 4‰; change in height decreased as salinities increased from 4‰.

Culm maintenance, reflected in the number of live and dead culms, differed significantly in salinity treatments higher than 27‰ (Table 3). However, the number of dead culms was least affected by increases in salinity. Tiller production began to significantly decrease at 35‰ (Table 3).

Discussion

Spartina densiflora is the dominant species in salt marshes at Humboldt Bay. Apparently introduced in the late 19th century from South America (Spicher 1984), *S. densiflora* has steadily increased in abundance in both established and disturbed salt marsh habitats (Barnhart et al. 1992). *S. densiflora* competes with a number of introduced and native plant species in Humboldt Bay salt marshes (Eicher 1987).
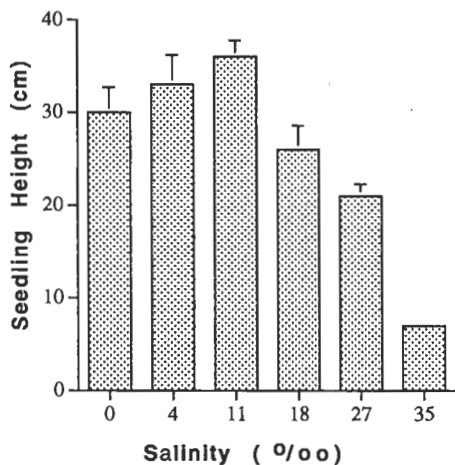

Fig. 4.   Height of seedlings in six salinity regimes. After 6 mo seedling height was greater in the salinity treatments 0‰, 4‰, 11‰, 18‰, and 27‰ than in 35‰.
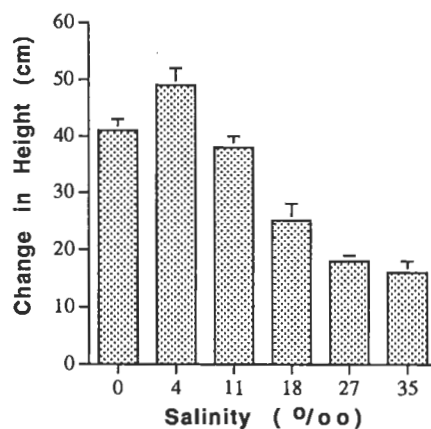

Fig. 5.   The change in height for adult plants in six salinity regimes: 0‰, 4‰, 11‰, 18‰, 27‰, 35‰. The greatest increases in height were for plants treated with water at 4‰.

TABLE 3. Average increase in number of dead culms, live culms, and tillers produced over 8 mo in mature greenhouse plants (n = 11/each of six salinity treatments). MANOVA indicates an overall difference in growth over the six salinity treatments (p < 0.0001). Group means (± SD) with the same superscript are not significantly different from one another (post hoc pairwise comparisons with Hotelling's T^2 and corrected for 30 multiple comparisons).

Salinity (‰)	Dead Culm	Live Culm	Tillers
0	0.7 ± 0.2[a]	0.6 ± 0.2[a]	6.4 ± 1.2[a]
4	0.9 ± 0.3[a]	0.2 ± 0.4[a]	6.5 ± 2.1[a]
11	0.7 ± 0.2[a]	0.1 ± 0.2[a]	5.6 ± 1.7[a]
18	1.2 ± 0.4[a]	−0.5 ± 0.3[a,b]	4.7 ± 1.4[a,b]
26	1.0 ± 0.4[a]	−1.5 ± 0.3[a,b]	4.0 ± 2.3[a,b]
35	1.2 ± 0.4[a]	−2.2 ± 0.4[b]	3.9 ± 1.5[b]

VEGETATIVE EXPANSION IN SALT MARSHES

In Humboldt Bay, natural disturbances such as wrack deposition generates areas bare of vegetation. Data we collected indicate that such bare areas are recolonized primarily from established vegetation surrounding the bare areas. Without competitors present, bare patches recover relatively quickly due to S. densiflora expanding laterally. Our observations suggest that recovering patches come to resemble the composition of adjacent, undisturbed salt marsh patches but with an overall increase in cover of S. densiflora. S. densiflora appears to promote its own expansion because it constitutes the majority of wrack that creates the bare areas. When surrounded by competitors in undisturbed areas, the expansion of S. densiflora culms by vegetative tiller production was much less. This confirms observations by us and Eicher (1987) that establishment and spread in undisturbed marshes is lower.

The significant increase in basal area without a corresponding increase in tiller production is due to two factors: tiller spacing and maintenance of adult culms. In plants surrounded by competitors, tillers were more tightly packed. In plants lacking competitors, tillers extended further from the parent plant. Additionally, for plants in bare areas, the combination of maintaining adult culms and producing new tillers results in greater lateral spread. Plants surrounded by competitors shed greater numbers of adult culms and new tillers generally replaced lost culms rather than contributing to the lateral expansion of the plant.

S. densiflora produces tillers throughout the year and this lack of a dormant period can confer competitive advantages. Potential competitors, such as Salicornia virginica, Jaumea carnosa, and Distichlis spicata, experience periods of dormancy and must resprout each year. In dense, established stands of S. densiflora, Eicher (1987) observed a decrease in the abundance and vigor of salt marsh species. Spicher

(1984) also noted that in well-established areas of S. densiflora at San Francisco Bay, exclusion of native Salicornia virginica and S. foliosa occurred.

REPRODUCTIVE CAPACITY AND POTENTIAL FOR GROWTH OF SEEDLINGS

At Humboldt Bay, seed production and viability are substantially higher in S. densiflora than S. foliosa and S. alterniflora (Crispin 1976; Spicher 1984; Callaway 1991). Thus, a potential for significant colonization by seed exists. However, only a few instances of seedling establishment were observed during the drought years of 1991 and 1992. During years of normal precipitation (1993–1995), substantially more seedlings were observed.

High salinity levels in salt marsh soils are likely to be the most significant environmental factor reducing germination success of S. alterniflora (Mooring et al. 1971), S. foliosa (Phleger 1971; Spicher 1984), S. patens (Sencca 1967), and other salt marsh species (Chapman 1974; Ungar 1978). Our results indicate that seeds of S. densiflora have the highest germination success at salinities less than 11‰ (Fig. 2). Germination success decreases as salinities rise to 35‰. Contrary to a finding by Mooring et al. (1971) S. densiflora seeds did not lose viability in dry storage at 0°C. Refrigeration was adequate to prevent desiccation, but viability might have been enhanced through storage in diluted seawater.

Growth of seedlings also is affected by the salinity regime, with fewer seedlings surviving at higher soil salinities (Table 2). A single seedling of 17 planted survived for 6 mo at 35‰. Seedling survival and growth was greatest in fresh water and 4‰, with modest survival in intermediate salinity regimes. Seedlings also may be quickly out competed by mature conspecifics or annual marsh species.

MECHANISMS OF ESTABLISHMENT AND EXPANSION

The relative contribution of vegetative growth and sexual reproduction to the successful maintenance of Spartina spp. populations remains controversial. Seneca (1974) and Woodhouse and Knutson (1982) concluded that seedling establishment constitutes the primary means of population expansion for S. alterniflora. For S. foliosa, establishment from seedlings is rare and colonization of bare substrates occurs by vegetative growth (Purer 1942; Phleger 1971; Callaway and Josselyn 1992).

Our results suggest that both modes of reproduction play a role in the expansion of S. densiflora in Humboldt Bay. Vegetative expansion is greater when S. densiflora is located in small bare areas. Vegetative expansion in mature, undisturbed marshes is more limited. Consequently, a more di-

verse plant community could tend to predominate in areas experiencing less disturbance.

At Humboldt Bay, we observed few seedlings in the field, recorded low germination rates and reduced seedling growth in seawater. Thus, recruitment by seed is probably less during years of low precipitation. Also, no seedlings were found in dense vegetation, suggesting that germination probably contributes little to the maintenance of *S. densiflora* in undisturbed marshes. However, seedling recruitment has been observed on bare, protected sediments during periods of significant freshwater influence. Periods of heavy rainfall, lower soil salinities, and disturbed areas with bare or sparsely vegetated soil may favor the establishment of seedlings.

While seed germination and seedling growth are limited at higher salinities, established mature plants are not as adversely affected at higher salinities. It does appear that established plants grow best at salinities between 0‰ and 11‰, but mature plants produce approximately the same number of tillers and culms and experience the same amount of die-back at salinities greater than 18‰ (Table 3). This suggests that if a seedling can become established, subsequent growth and expansion can readily occur at higher salinities.

In summary, our results suggest that the level of disturbance, competition and salinity regime of salt marsh soils will have significant effects on the establishment and expansion of *S. densiflora*. *S. densiflora* produces an abundance of viable seeds which disperse widely via tidal currents. Even though seed germination is limited by higher salinities, the capability of *S. densiflora* to germinate during brackish conditions enables it to colonize bare or disturbed areas with significant freshwater influence. In undisturbed marshes, there are fewer opportunities for *S. densiflora* to establish within dense cover. However, phenological advantages (e.g., no dormant period) can lead to incremental increases in circumference. The physiological plasticity of established, mature plants also enables it to tolerate a wide range of salinities and expand laterally when marshes are disturbed by wrack deposition or human activities.

S. densiflora's ability to rapidly expand in bare areas has implications for marsh mitigation and restoration activities within Humboldt Bay. Mitigation sites often have large areas of bare substrate. In mitigation sites where natural colonization of salt marsh species is allowed to occur, monocultures of *S. densiflora* may result. Moreover, any decrease in salinity could allow *S. densiflora* seedlings to establish. If the goal of the restoration project is to establish a heterogeneous community of salt marsh plants, relying on natural recruitment may

not be the best approach. To offset the dominance of *S. densiflora* in bare areas, active seeding or planting of native salt marsh plants should be undertaken. Once native marshes are established the relative expansion rate of *S. densiflora* may be slowed.

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