Nitrogen Addition Could Shift Plant Community Composition in a Restored California Salt Marsh

Katharyn E. Boyer1,2
Joy B. Zedler1

Abstract

At a salt marsh restoration site, fertilizer trials to improve height growth of Spartina foliosa (a C4 perennial grass that can reach 140 cm) appeared to favor Salicornia bigelovii (an annual C3 succulent under 40 cm tall) where the two species co-occurred on the marsh plain. This observation prompted a field experiment to examine the potential for nitrogen (N) addition to shift community composition. Without N addition, total stem length and stem density of S. foliosa did not respond to the presence or absence of S. bigelovii. But where N was added, S. foliosa growth increased only where S. bigelovii was removed from plots. S. bigelovii responded strongly to fertilizer, with mean heights matching those of S. foliosa and 600% increases in biomass, branching, and seed production (to more than 1 million seeds/m²). Soil N also increased seasonally where S. bigelovii was present, suggesting that this species may aid accumulation of N at restoration sites with poor soils. S. foliosa growth is greatest at lower elevations along tidal creeks where it occurs alone. Beyond creek edges, where S. bigelovii and other potential competitors occur, S. foliosa is unlikely to grow tall even with N addition. Thus, there is little point in trying to force mixed-species stands to provide tall S. foliosa for nesting by an endangered bird, Rallus longirostris levipes (the Light-footed Clapper Rail). A marsh construction design that maximizes tidal creek edges is thus recommended when restoration goals include providing habitat for clapper rails.

Introduction

Nitrogen limitation, implied by increased growth after fertilizer additions, is common of salt marsh plants on the east coast (Gallagher 1975; Valiela et al. 1985; Osgood & Zieman 1993), west coast (Covin & Zedler 1988; Gibson et al. 1994; Parsons & Zedler 1997; Boyer & Zedler 1998), and gulf coast (Patrick & DeLaune 1976; de la Cruz et al. 1981; DeLaune & Pezeshki 1988) of the United States. Where coastal wetlands are constructed from sandy upland soils or dredge spoils, sediments are typically low in organic matter and nitrogen (N) pools (Broome et al. 1975; Parnell et al. 1978; Lindau & Hossner 1981; Craft et al. 1988; Webb & Dodd 1989; Langis et al. 1991) and therefore provide even less of the mineral nutrition needed by plants. Inorganic fertilizers—soluble forms like urea or ammonium nitrate or slow-release forms like sulfur-coated urea—are often used to amend soils at the time of planting or repeatedly applied until plants are well established at a restoration site (Woodhouse & Knutson 1982; Broome 1990); less commonly, organic forms such as kelp are incorporated into soils (Boyer et al. 1996; Zedler 1996). Sometimes, N additions are enlisted at a restoration site after plants are established but still lack the growth characteristics needed to provide important habitat functions (Zedler 1993; Boyer & Zedler 1998). Similarly, fertilizers may be used at restoration sites to ensure the persistence of annual plants with high interannual variation in population size (Parsons & Zedler 1997).

While nutrient addition is commonly recommended for restoration sites, there is a paucity of research into its effects on species interactions within the restored plant community. In natural marshes, fertilization experiments have been performed mainly where plants occur as monocultures—for example Spartina alterniflora (smooth cordgrass) on the east and gulf coasts of the United States. The few studies of fertilization effects on salt marsh plant communities in natural marshes report resultant shifts in community composition (Valiela et al. 1975, 1985; Jefferies & Perkins 1977). Species differ in N uptake and use efficiency (Shaver & Melillo 1984; Bridgham et al. 1995) as well as growth habit and phenomenology (Grime 1973), so altering the soil nutrient status might affect a species’ relative success within a community. The effects of nitrogen additions might be amplified in constructed salt marshes, where soils can be especially N-poor (Boyer & Zedler 1998).

1Pacific Estuarine Research Laboratory, San Diego State University, San Diego, CA 92182–0057, U.S.A.
2Current address: Department of Biology, University of California, Los Angeles, Los Angeles, CA 90095–1606, U.S.A., email katboyer@ucla.edu

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Like the studies of *Spartina alterniflora* in natural marshes (Gallagher 1975; Chalmers 1979; Osgood & Zieman 1993), our recent N-addition experiments in both constructed and natural salt marshes were designed to assess effects on only one species, *Spartina foliosa* (Pacific cordgrass; Gibson et al. 1994; Boyer & Zedler 1998). This C₃ perennial grass dominates the lowest elevations of tidally flushed marshes of southern California. It is a major target for restoration efforts, because tall *S. foliosa* is used for nesting by an endangered bird, *Rallus longirostris levipes*, the Light-footed Clapper Rail (Massey et al. 1984; Zedler 1993). In San Diego Bay, however, transplanted *S. foliosa* is usually too short for clapper rail nesting (Zedler 1993). With a single season of N fertilization, transplanted *S. foliosa* matches the canopy heights and densities of reference natural marshes, but annual fertilization during the growing season is required to sustain tall canopies (Boyer & Zedler 1998).

To achieve tall *S. foliosa* in areas large enough to serve as home ranges for clapper rails in constructed marshes in San Diego Bay, fertilization of 400-m² areas has been proposed. While *S. foliosa* occurs by itself along creek banks and in shallow tidal pools, it is mixed with other species, including *Salicornia bigelovii* (annual pickleweed), *Salicornia virginica* (pickleweed), and *Batis maritima* (saltwort), on the marsh plain at higher elevations. Little is known about how these species might respond to fertilization or how they might affect the ability of *S. foliosa* to scavenge nutrients. One previous study (Covin & Zedler 1988) examined fertilization effects on a mixture of *S. foliosa* and *S. virginica* in a natural marsh (Ti-juana Estuary, 32°34’N, 117°7’W). With N additions, *S. foliosa* increased in biomass when *S. virginica* was removed, but not when the species were grown together (Covin & Zedler 1988). *S. virginica* was shown to out-compete *S. foliosa* for added N.

Our preliminary trials of mixed-stand fertilization in constructed marshes suggested that *S. bigelovii*, an annual C₃ succulent, may also be a vigorous competitor with *S. foliosa*, becoming similar in height to *S. foliosa* and highly branched with added N (K. E. Boyer, personal observation). This response was not expected from an annual that usually has low abundance and short canopies (~40 cm maximum) in natural marshes, compared to the clonal, perennial *S. foliosa*, which grows densely and quite tall (up to ~140 cm). Even though *S. bigelovii* is common in constructed marshes with more open plant canopies, it generally remains shorter than *S. foliosa* and appears to have little effect on *S. foliosa* establishment or growth (K. E. Boyer, personal observation). Although morphological variability is quite high in *S. bigelovii* (K. E. Boyer and J. B. Zedler, personal observation), it is most often found as simple erect spikes with little or no branching. In our fertilizer trials, it was highly branched and robust, suggesting that interactions between *S. bigelovii* and *S. foliosa* may be affected by N enrichment at constructed marshes.

In this study, we established a field experiment to examine the relationship between *Spartina foliosa* and *Salicornia bigelovii* at a constructed wetland. We transplanted *S. foliosa* into a constructed marsh with abundant *S. bigelovii* shortly after the latter began to germinate in spring. We tested the response of the two species to N additions, predicting that N would favor *S. bigelovii*, based on our previous observations of its rapid and large response to N additions in this constructed marsh. We predicted that *S. foliosa* growth would be similar with or without *S. bigelovii* present when no N is added. We further predicted that *S. foliosa* growth would be reduced when mixed stands of the two species are fertilized.

Our experimental treatments included growing *S. foliosa* in plots with *S. bigelovii* present, and in plots with *S. bigelovii* excluded either by hand-clearing (clipping) or covering with black plastic. Within each of these “exclusion treatments,” plots either received N additions throughout the growing season or were not fertilized. These treatments allowed examination of fertilization effects on the two species grown together and on *S. foliosa* grown alone.

**Methods**

**Study Location**

This study was performed at Sweetwater Marsh National Wildlife Refuge (hereafter called the refuge), which contains the largest remaining area of wetlands on San Diego Bay. It is located between 24th Street in National City and E Street in Chula Vista, California (32°40’N, 117°5’W; Fig. 1). The 128-ha refuge is composed mostly of intertidal salt marsh, with both natural and constructed areas. The marshes are tidally inundated in a mixed semi-diurnal pattern (one tidal cycle is more extreme than the other each day), with a maximum spring tide range of 3 m.

Within the refuge, Connector Marsh is a 4.9-ha wetland created to mitigate for damages incurred during construction of a highway and a flood-control channel (Swift 1988). Connector Marsh was excavated from dredge spoils in 1984, and most of the area was planted with salt marsh vegetation in 1985. The area of our field experiment was not planted until 1992. Soils derived from the dredge spoil are coarse, with 48–92% sand and only 5–20% clay in 10-cm deep cores collected adjacent to this experiment (Pacific Estuarine Research Laboratory [PERL], unpublished data from May 1996), but a finer layer of sediment is beginning to accumulate at the surface throughout the constructed marsh (PERL, unpublished data from March 1995). Connector Marsh sediments within cordgrass stands were composed of
about 2.5% organic matter in 1990, compared to about 6.5% organic matter in the clay loam soils of the natural marsh, Paradise Creek (PERL, unpublished data).

Site Preparation

The experiment was set up on 4–5 April 1996 in Connector Marsh, both north and south of the flood-control channel (Fig. 1). Five blocks of experimental plots were laid out in areas where seedlings of *S. bigelovii* were well established. Elevations were at the high end of the *S. foliosa* distribution. Each block was composed of six 0.25-m² circular plots. Four of the blocks were linear, with 2-m buffers between plots (Fig. 2); one block had two rows of three plots, 2 m apart.

The area of each plot was cleared of all vegetation other than *S. bigelovii* (including existing *S. foliosa*) by digging up the plants with roots or rhizomes and intact soil. Vegetation was removed from within each plot and within a 20-cm radius outside the plot.

*S. foliosa* for transplanting into the plots was selected from nearby areas of Connector Marsh (within the south end for plots in the south and from the north end for those in the north). Our criteria for selecting the *S. foliosa* were that there be no signs of rodent herbivory or insect larvae that “mine” the leaves (*Incertella* sp.) or bore within the stems (*Thaumatopsis fieldellus*). Low densities (<10 individuals) of *Haliaspis spartina* (an armored scale insect) and/or *Prokelisia dolus* (a plant hopper) were permitted, as these herbivores are too common to avoid. We selected uniform clumps of new *S. foliosa* shoots for transplanting into each plot; clumps had a mean stem density of 4.3 ± 0.1, a mean stem height of 25.3 ± 0.7 cm, and a mean total stem length of 1.1 ± 0.03 m. Soil plugs approximately 15 cm in diameter (~0.015 m²) and 25 cm deep were expected to allow sufficient root and soil mass to ensure survival. Plugs were dug with a narrow shovel inserted straight down around the circumference of the plug. Each plug was then carried directly to the hole pre-dug in each plot, planted, and watered with about 4 liters of water from a nearby channel (salinity approximately 34%).

Small-mammal herbivory on *S. foliosa* is prevalent in local marshes, especially south of the flood-control channel and adjacent to the freeway (near three of our blocks; Fig. 1). To reduce herbivory in our experimental plots, chicken wire (0.5 m tall) was secured around each plot with 15-cm metal staples typically used to secure jute matting (Fig. 2). Fences of this height were expected to reduce but not prevent herbivory. Evidence of her-
Experimental Treatments

On 22 April, we randomly assigned the treatment conditions to five blocks in our 3 × 2 factorial experiment. Three S. bigelovii exclusion treatments were used to test the effects of S. bigelovii presence or absence on S. foliosa response variables. In the first, S. bigelovii was left in the plots (“no-exclusion” treatment). Where growth was sparse or patchy, additional individuals were transplanted into the plots to match densities (visually estimated) of the surrounding area. In the second, existing S. bigelovii was removed by clipping at the ground level (“clearing” treatment). Because previous work (Zedler 1975) found S. bigelovii to re-invade after removal, these plots were observed carefully so that new recruits could be removed quickly. In the third treatment we excluded S. bigelovii by clipping it at the sediment surface, then securing black plastic over plots using 15-cm-long metal staples (“plastic” treatment). A hole approximately 0.03 m² was cut in the center to allow transplanted S. foliosa to grow without confinement. A metal staple was used to poke holes into the plastic to increase air movement below.

The two N-addition treatments consisted of fertilizing with urea (CO(NH₂)₂, 46% N by weight) or not fertilizing (control). Fertilizer was hand-broadcast every 2 weeks at low tide through 4 August 1996. On each of the eight dates, 8.2 g (15 g N/m²) of urea fertilizer were sprinkled evenly into the randomly assigned plots. Care was taken to spread fertilizer only within the 0.25-m² plots. In the plastic/fertilized plots, the plastic was temporarily removed while N was added, then re-secured.

Response Variables

S. foliosa heights and densities were measured in each plot bimonthly (24 May, 31 July, and 26 September 1996). Total stem length (TSL) was determined by summing the heights of each culm from the base to the tip of the longest leaf, a nondestructive method of estimating biomass (Zedler 1983). All stems within 0.25 m² were sampled, as new shoots spread outside the original footprint of the transplanted plug. Individual stem lengths were converted to biomass by means of a regression developed from randomly selected stems in three areas of Connector Marsh on 14 August 1996 [log(biomass) = 1.683 * log(stem length) − 2.743; n = 60; adjusted R² = 0.95]. This conversion was performed to examine N standing crop (biomass * % foliar N) and the percentage of added N incorporated into tissues; N analysis is described below. In addition, scale insects were monitored in the plots, because their abundance may relate to S. foliosa N content, height, or stress (Boyer & Zedler 1996). Scale insects were estimated by abundance classes: 0, no individuals; 1, 1–9; 2, 10–99; 3, 100–999; and 4, ≥ 1000, as in Boyer and Zedler (1996).

S. bigelovii biomass was estimated from height data on 24 May and 31 July and measured directly on 26 September 1996. On the first two dates, two circular 0.01-m² quadrats were placed twice within each plot, 10 cm from both the north and south edges, and plants were measured from the sediment surface to the highest branch tip. To convert these stem lengths to biomass, regressions were developed from stems collected outside the experiment (see below). Two separate regression equations were developed to account for a seasonal increase in S. bigelovii branching. Stems collected on 6 June were used to develop a regression for converting the 24 May stem heights to biomass, and stems collected on 27 August were used to convert the 31 July measures. For the 6 June stem collection, unfertilized plants were clipped at the sediment surface within three 0.01-m² circular quadrats spaced evenly along a line 2 m from each experimental block (total of 15 quadrats, 265 stems); stems were clipped within an additional three quadrats (129 stems) placed randomly in a nearby fertilized area receiving the same rate of N addition but not related to this experiment (Fig. 1); unfertilized and fertilized measures were combined for the best model fit [log(fresh mass) = 1.652 * log(height) − 1.939; adjusted R² = 0.88, p = 0.0001]. Fresh mass was converted to dry mass with a separate regression [log(dry mass) = 0.162 * log(fresh mass) + 0.058; n = 243, adj. R² = 0.97, p = 0.0001]. For the 27 August collection, stems within five 0.01-m² quadrats were clipped from randomly located areas in both fertilized and unfertilized areas nearby this experiment (Fig. 1). The best model fit was found by combining fertilized and unfertilized plants [243 stems; log(dry biomass) = 1.916 * log(height) − 3.113; adj. R² = 0.82, p = 0.0001].

Direct measures of biomass in the experimental plots were made on 26 September 1996; stems within two 0.01-m² circular quadrats (at the east and west side of each plot) were clipped, rinsed, dried, and weighed. Also
at that time, two quadrats of S. bigelovii were clipped just outside each plot (on the east and west side), because increased growth was apparent up to 20 cm from the outside edge of some of the fertilized plots. Nearly all of the plants collected for biomass regressions (and N content, see below) had developed fruits by the September collection dates, but seeds had not yet matured or been released from the seed heads.

Also on 26 September, aboveground tissue was collected to determine total Kjeldahl nitrogen (TKN) content inside the plots for both species and also outside the plots for S. bigelovii. For S. foliosa, one or more green leaves from each stem (depending on the number of stems present) was clipped, returned to the lab, rinsed, dried at 60°C to a constant mass, ground in a Wiley Mill and analyzed for TKN (QuickChem Method 13–107–06–2–D) with a Lachat autoanalyzer (model #2100–000). For S. bigelovii, the clipped plants returned to the lab for biomass measures were sorted into woody stems and “tips” (succulent spikes of stem, bract, and inflorescence tissue, including immature seeds) and analyzed for TKN after being processed in the same manner as the S. foliosa. A portion of the material was dried at 105°C, weighed, then ashed in a muffle furnace at 500°C to determine ash-free dry mass. N concentrations were then calculated based on ash-free dry mass of leaf (S. foliosa) or tip (S. bigelovii) tissue.

While S. foliosa spreads clonally and rarely recruits from seed (Zedler 1981), seed production is an annual necessity for S. bigelovii. S. bigelovii seed production, with and without N additions, was estimated using regression equations based on inflorescence length and the number of nodes (six seed cavities per node) in each. On 11 December 1996, plants were clipped within two 0.01-m² circular quadrats at the north and south end of the no-exclusion plots, then combined. Inflorescence length and the number of nodes were recorded for a portion of the plants; separate regressions were developed for plants that were unfertilized (number of nodes = 2.533 * spike length − 0.171, n = 104, adj. R² = 0.939, p = 0.0001) and fertilized (number of nodes = 2.672 * spike length + 1.043, n = 118, adj. R² = 0.939, p = 0.0001). These regression equations were used to predict the number of seeds (multiplying the number of nodes by six) from lengths of an additional 1500+ spikes. In addition, to compare the degree of branching with and without fertilization, the number of branches on each individual plant was counted; a shoot with no branches = 0.

On 9 April 1996, initial soil conditions were sampled with three soil cores (5 cm diameter, 10 cm deep) collected at regular intervals along each block (outside plots). On 27 September, two soil cores (same dimensions) were taken within each plot. In both cases, soils were dried at 50°C to a constant mass, ground with a mortar and pestle, and analyzed for TKN (as above).

Both April and September soils were analyzed for salinity with saturated soil pastes (Richards 1954); a 10-cc plastic syringe (without needle, with two layers of #2 Whatman filter paper cut to size) was used to express soil water onto a temperature-compensated refractometer (Reichert [now Leica] model #10419). In addition, soils collected in September were analyzed for KCl-extractable N (NO₃⁻ + NO₂⁻ and NH₄⁺) (American Public Health Association et al. 1992).

Statistical Analyses

For S. foliosa total stem length, density, maximum height, mean height, N concentration, and standing N crop, two-factor analysis of variance (ANOVA) was performed (with block and treatment as factors). The mean squared error (MSE) produced in each ANOVA was used in three mutually orthogonal comparisons to test three a priori hypotheses. First, under N-enriched conditions, we expected S. foliosa growth and N concentration to be different (greater) where S. bigelovii was excluded than where S. bigelovii was grown along with S. foliosa. Second, without N additions, we expected the S. foliosa response variables to be similar whether or not S. bigelovii was present. Finally, we expected the two S. bigelovii exclusion treatments (clearing and plastic) to result in different S. foliosa responses; the S. foliosa in the plastic treatment could experience physical limits on clonal spread, thereby reducing growth or, alternatively, cleared plots could have reduced S. foliosa growth due to repeated invasion by S. bigelovii. Orthogonal contrasts were made using Systat (version 5.2.1 for Macintosh). S. foliosa TSL and stem density were log-transformed to meet the assumptions of ANOVA.

We used three-factor ANOVA (with block, N treatment, and exclusion treatment as factors) to examine soil N and salinity, scale insect abundance on S. foliosa, and S. bigelovii biomass and N concentration just outside plots. Interactions between N and exclusion treatment were not significant unless otherwise noted. We examined S. bigelovii biomass, density, TKN, and seed production using two-factor ANOVA (with block and N treatment as factors). Data were transformed as necessary to meet the assumptions of ANOVA: log(x+1) on sediment TKN and NO₃⁻ + NO₂⁻ data, and log(x) on S. bigelovii biomass and seed production. Super-ANOVA (Version 1.11, Abacus Concepts, Inc., 1991) was used for these analyses.

Results

Exclusion Treatments

The two methods of S. bigelovii exclusion (clearing and plastic) worked similarly well in keeping S. bigelovii out.
of plots. No seedlings emerged from beneath the black plastic and, in the clearing treatment, additional S. bigelovii recruits rarely needed to be removed, contrary to previous work by Zedler (1975).

S. foliosa growth and N concentrations were similar in plots where S. bigelovii was excluded by either method (orthogonal contrasts, \( p > 0.05 \)). Though S. foliosa total stem length was similar, clonal establishment of new shoots in the plastic treatment appeared to be restricted by the hole cut in the center of the plastic. Only two out of 10 plots covered with black plastic had S. foliosa shoots growing beneath the plastic: four in one plot and one in another. In contrast, the hand-cleared treatment plots had from 1 to 28 new recruits (mean and standard error: 4.1 \( \pm \) 2.7) as close as 5 cm from the outside edge of the plots. Black plastic limited spatial spread by S. foliosa rhizomes, but biomass was similar with either exclusion treatment.

Because the plastic and clearing treatments resulted in similar plant responses, data are presented in the next sections as averaged values of the two S. bigelovii exclusion treatments (“– Sb”). The two treatments did produce some differences in soil responses and are kept separate when those results are reported.

**Spartina foliosa**

Throughout the growing season, without N additions, S. foliosa total stem length and stem density were similar regardless of the presence of S. bigelovii (Fig. 3; orthogonal contrasts, \( p > 0.05 \)). Only where N was added did S. foliosa growth respond to S. bigelovii exclusion; S. foliosa total stem length and stem density were significantly higher in both July and September where S. bigelovii was excluded (Fig. 3; orthogonal contrasts, total stem length \( p = 0.037 \) in July and 0.003 in September; stem density \( p = 0.013 \) in July and 0.003 in September).

S. foliosa maximum heights were similar regardless of treatment (Fig. 3; orthogonal contrasts, \( p > 0.05 \)). Mean stem height was similar in all months but July, when plots with S. bigelovii present had increased S. foliosa mean stem height whether or not N was added (Fig. 3; orthogonal contrasts testing effect of S. bigelovii presence with N additions \( [p = 0.021] \) and without \( [p = 0.030] \)). There were no differences in S. foliosa mean stem heights by September (Fig. 3). Mean heights averaged less than 30 cm overall, an increase of only about 5 cm during the growing season.

S. foliosa foliar N did not differ regardless of N or exclusion treatment when sampled in September (Fig. 4; orthogonal contrasts, \( p > 0.05 \)). S. foliosa leaf tissue was 87% organic matter, so tissue N concentrations based on ash-free dry mass were only slightly greater than those based on total leaf biomass (Fig. 4). S. foliosa standing crop of N did not increase with N additions, regardless of S. bigelovii exclusion. Our September sampling detected 0% accumulation of added N in S. foliosa aboveground tissues when S. bigelovii was present, and less than 1% when S. bigelovii was excluded.

No inflorescences were produced by S. foliosa in plots, even though about 10% of culms are normally flowering in September at lower elevations along creeks within both Connector Marsh and the natural marsh at nearby Paradise Creek (PERL, unpublished data from 1993 and 1996). The influences of N addition and competition with S. bigelovii thus had no known effect on seed production.

Two transplants showed evidence of lepidopteran stem borers (presumably *Thaumatopsis fieldellus*) as early as May, and by our July sampling date all culms were brown and mostly decomposed in both plots. The two affected plots were side by side within one block; one was an unfertilized plot with mixed species, and one was a fertilized plot with S. bigelovii excluded by plastic. Thus, stem-borer herbivory did not appear to relate to treatment, and these two plots were dropped from the July and September analyses. A few stems developed dipteran leaf miner (*Incertella* sp.) damage not visible at the time of transplanting, but this did not appear to affect S. foliosa survivorship. Scale insect abundance on S. foliosa did not differ by treatment on any date (three-factor ANOVA, \( p > 0.05 \)). The presence of
other insects was never great enough to warrant monitoring. There was no evidence of rodent herbivory inside the plot fences, but nearly 50% (54/115 culms) of *S. foliosa* stems sampled outside the plots in south Connector Marsh showed rodent damage on 6 June 1997. Damage was rare near the plots in north Connector Marsh (1/145 culms).

**Salicornia bigelovii**

Where *Salicornia bigelovii* was present in plots (i.e., not excluded by clearing or plastic), its aboveground biomass was similar with or without N additions in late May, after fertilizor had been added for one month (Fig. 5). By late September, however, fertilized *S. bigelovii* mass had increased by 600% over controls (Fig. 5; two-factor ANOVA, \( p = 0.0008 \)). The rate of biomass increase with fertilization was much larger in late summer (July to September) than earlier (May to July). This is not an artifact of the July biomass having been estimated from stem lengths using a late-August regression equation. In fact, with increased branching during the growing season, this equation may have overestimated mass in July, suggesting that the increase in mass from July to September may have been even more dramatic than that shown in Figure 5.

*S. bigelovii* stem density was significantly lower with fertilization than without in late May and late July (two-factor ANOVA, \( p = 0.0102 \) and \( p = 0.0385 \), respectively) but was not different in September (Fig. 5). Greater branching with fertilization was observed as early as May (but not measured until December) and may have related to lower densities in fertilized plots on the first two dates. *S. bigelovii* densities declined during the season regardless of N enrichment, especially in the controls (declined from 3460 ± 660 stems/m² in May to 1510 ± 210 stems/m² in September; Fig. 5).

Both *S. bigelovii* maximum height and mean height were similar by treatment in late May, but N addition resulted in 200% increases over controls in July and September (Fig. 5). By September, mean heights were similar to those of *S. foliosa* (Figs. 3 & 5).

*S. bigelovii* present in plots trapped N and reduced losses to the surrounding area; a significantly lower biomass response was detected just outside plots (within 15–20 cm) when *S. bigelovii* was present inside than when it was excluded (Fig. 6; three-factor ANOVA, \( p = 0.0029 \)). Overall, biomass outside plots was greater when N was added inside than when it was not (three-factor ANOVA, N treatment \( p = 0.0001 \)).

Foliar N in the succulent tissues did not differ with fertilization (Fig. 6), but the strong biomass response
suggests that there was greater N uptake and conversion to biomass with fertilization. Succulent tissue of *S. bigelovii* contained only 49% organic matter, so N concentrations based on ash-free dry mass were about two times greater than those based on the full dry mass of succulent tissue (Fig. 6). Consequently, tissue N concentrations of *S. bigelovii* based on ash-free dry mass approach those of *S. foliosa* (Fig. 4). Despite a differential biomass response outside the plots, foliar N was similar by treatment and comparable to the in-plot foliar N levels (Fig. 6).

The N added to plots resulted in an approximately eight-fold increase in the *S. bigelovii* standing crop of N by late September (14.9 g N/m² with N additions versus 1.9 g N/m² without). Outside plots, standing N crop increased about two-fold with N additions inside; like the biomass data, these results indicate losses of N outside the plots. Only about 11% of the 120 g N/m² added was recovered by aboveground tissues if the full amount is assumed to have stayed within plots; knowing that there were losses, however, and that the standing N crop inside plots increased by about four times more with N additions than the adjacent areas, the percent of N taken up by *S. bigelovii* aboveground tissue within plots may have been closer to 14%.

Seed production of *S. bigelovii* had greatly increased with fertilization when estimated in mid-December (two-factor ANOVA, *p* = 0.0034). With N addition, *S. bigelovii* in mixed plots produced over 1 million seeds/m² compared to about 200,000 seeds/m² in plots where no N was added (Fig. 7). The length of inflorescence spikes was similar (~4 cm; Fig. 7), but about six times more spikes were produced with fertilization. Fertilization had a strong effect on the degree of *S. bigelovii* branching; there was about six times greater branching in fertilized plots than in controls when assessed in mid-December (Fig. 7). Seed production and the degree of branching appeared to be closely linked (Fig. 7).

**Soils**

Relative to initial mean TKN (which did not differ among plots), soil N concentrations in September increased where *S. bigelovii* was present, especially with N additions (Fig. 8). Soil TKN in September was significantly greater where *S. bigelovii* was present than where

![Figure 6. Aboveground biomass and nitrogen concentration of *Salicornia bigelovii* inside experimental plots (only in two treatments) and just outside, 26 September 1996. Plants were clipped within two 0.01-m² quadrats inside plots or immediately outside plots. *n* = 5; error bars represent ± 1 SE.](image)

![Figure 7. *Salicornia bigelovii* seed production (estimated from regression between inflorescence length and number of seeds), degree of branching (a shoot with no branches = 0), and mean of all inflorescence lengths, under control (C) and nitrogen enriched conditions (+N). Plants were clipped within two 0.01-m² quadrats in each plot on 11 December 1996. *n* = 5; error bars represent ± 1 SE.](image)
it was excluded ($p = 0.005$). A significant interaction between $S. \text{bigelovii}$ exclusion treatment and $N$ treatment ($p = 0.01$) warranted examining these factors more closely (Table 1). Where $S. \text{bigelovii}$ was present, N additions resulted in higher TKN. Where $S. \text{bigelovii}$ was excluded, the same increasing trend with fertilization was apparent in the plastic treatment, but the pattern was reversed where $S. \text{bigelovii}$ was cleared from plots. Hence, the interaction resulted from a differential soil TKN response to N additions where $S. \text{bigelovii}$ was hand-cleared from plots.

Despite a difference in fertilization effect on total soil N in the two treatments where $S. \text{bigelovii}$ was excluded, $S. \text{foliosa}$ responded similarly in biomass and N content in the two treatments (see beginning of Results section). Soil total N is predominately organic N, while inorganic N is what is readily available to plants. Inorganic N (as NH$_4^+$ and NO$_3^-$ + NO$_2^-$) increased with N addition (Fig. 8; three-factor ANOVAs, $p = 0.012$ and $p = 0.003$, respectively) but was similar whether or not $S. \text{bigelovii}$ was present.

Soil salinities were similar initially but were higher in the fertilized plots than in the controls when measured at the end of the experiment (Fig. 9; three-factor ANOVA, $p = 0.011$ for N treatment). Still, soil salinities remained within the range previously found for low intertidal

![Figure 8. Sediment total Kjeldahl N (TKN) and inorganic nitrogen (as NH$_4^+$ and NO$_3^-$ + NO$_2^-$) by treatment, 27 September 1996. $n = 5$; error bars represent ± 1 SE. Top figure also shows mean initial soil TKN (9 April 1997), with shaded area representing ± 1 SE.](image1)

![Figure 9. Soil salinity by treatment, 27 September 1996. $n = 5$; error bars represent ± 1 SE. Figure also shows mean initial soil salinity (9 April 1997), with shaded area representing ± 1 SE.](image2)

### Table 1. Mean soil total Kjeldahl nitrogen values (27 September 1996) for interpretation of the interaction between nitrogen treatment (+N or no addition = C) and Salicornia bigelovii exclusion treatment (+/-Sb).*

<table>
<thead>
<tr>
<th>Exclusion treatment</th>
<th>$+\text{Sb}$</th>
<th>$-\text{Sb (Clear)}$</th>
<th>$-\text{Sb (Plastic)}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>C (no N added)</td>
<td>0.140</td>
<td>0.121</td>
<td>0.090</td>
</tr>
<tr>
<td>$+N$</td>
<td>0.151</td>
<td>0.103</td>
<td>0.138</td>
</tr>
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</table>

*Total Kjeldahl nitrogen data in mg N/g dry soil were transformed by log($x+1$).
marsh in this region (Zedler 1983; Boyer & Zedler 1998). Plots covered with black plastic appeared to have lower soil salinities than plots where S. bigelovii was present and where it was excluded by hand-clearing (Fig. 9). Soil salinities generally increase during the growing season (Boyer & Zedler 1998) because little or no rainfall occurs during the warm summer months and evaporation is high (San Diego Lindbergh Field long-term data). But the black plastic may have acted as shade, reducing evaporation and salt accumulation (Bertness et al. 1992; Bertness & Shumway 1993). In contrast, the plots with the greatest plant cover and biomass, the fertilized no-exclusion plots, ranked highest in soil salinity (Fig. 9), possibly due to greater evapotranspiration.

Discussion

While short annual plants are unlikely to have an advantage over tall perennials in established communities, the results of this experiment support our hypothesis that Salicornia bigelovii is favored over Spartina foliosa when N is added to stands of both species in a developing salt marsh. Fertilization greatly increased S. bigelovii biomass, maximum height, mean height, degree of branching, and reproductive potential. Morphological changes in S. bigelovii may increase competition with S. foliosa for light, space, nutrients, or other resources. In the absence of N addition, S. foliosa total stem length and densities did not respond to the presence or absence of S. bigelovii in plots. With N addition, these S. foliosa growth parameters increased only where S. bigelovii was excluded from plots. Our results suggest that fertilizing to improve S. foliosa growth for clapper rail nesting may be successful only in pure S. foliosa stands, which occur mainly along the banks of tidal creeks and channels. We recommend that designs for new marsh construction maximize tidal creek edges when restoration goals include habitat for clapper rails.

Why fertilization would favor a C₃ species, Salicornia bigelovii, over a C₄ species, Spartina foliosa, in the warm climate of southern California is not obvious. Others have found a similar shift from C₄ to C₃ species under N-enriched conditions. In a study of perennial grasses by Wedin and Tilman (1996), the high N-use efficiency (NUE) of the C₄ species (203) relative to the C₃ species (107 and 78 for the two species) was implicated in the shift; when fertilizer was added, the advantage of the species with efficient N use declined (Wedin & Tilman 1996). In contrast, we found NUE to be somewhat higher in the C₃ species S. bigelovii (51–56), than in the C₄ species S. foliosa (31–42). Our calculation of NUE used a simplified method (the inverse of the N concentration; Chapin 1980) best suited to annual species, because perennials increase their efficiency through re-translocation of nutrients during senescence (Vitousek 1982; Bridgham et al. 1995). As we examined NUE post hoc, we lacked the more detailed measurements necessary to best determine a perennial’s NUE (Vitousek 1982; Bridgham et al. 1995), but S. foliosa is likely to be more efficient at utilizing N than our estimate suggests.

Differences in life history strategies between annual and perennial species can factor into their interactions. Annual species can have faster growth rates and generally put more resources into sexual reproduction, but perennial species must allocate resources to storage for the next year’s growth. Generally speaking, for an annual to be favored over a perennial species over time, it must have extremely high fecundity. In our experiment, Salicornia bigelovii seed production was very high, reaching over 1 million seeds/m² with N additions. Under controlled conditions, nearly 100% of seeds produced by S. bigelovii germinate (PERL, unpublished data), so the impact of the tremendous volume of viable seed produced through N addition could be large. Still, S. bigelovii densities are probably not normally limited by seed source, considering the high seed production and plant density without N addition (~200,000 seeds/m² and 1500–3500 plants/m²). The fact that densities declined during the season suggests that more seedlings established than there were resources or space to support them. In marshes with mature perennial canopies and developed root systems, available space for colonization may be a serious limitation to S. bigelovii’s success; this limitation is reduced in newly restored marshes with open canopies.

Because we did not sample S. foliosa tissues belowground, we are not able to assess conversion of N into long-term storage products. Accumulation of added N in S. foliosa aboveground tissues was extremely low (0–1%). This is probably because S. foliosa was planted only in the center 0.02 m² of the 0.25-m² plot, and root growth during the season may have been insufficient for interception and absorption of nutrients within the full area of the plot. In a previous study, S. foliosa along creeks in constructed and natural areas of the Sweetwater Marsh National Wildlife Refuge incorporated much more of the added N into aboveground tissues after the same rate and total quantity of N addition (Boyer & Zedler 1998). In that study there was much greater S. foliosa standing crop (total stem length without N additions = ~33 m/0.25 m²; Boyer & Zedler 1998) than in the current study (total stem length = ~2 m per 0.25-m² plot), and presumably much greater belowground tissues with which to exploit available nutrients. In view of the low N incorporation by aboveground S. foliosa tissues in this study, we assume that belowground accumulation of added N was similarly low (though not measured).

Still, belowground storage and recycling may ultimately result in improved S. foliosa growth. Tissue N...
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