EFFECTS OF NITROGEN ADDITIONS ON THE VERTICAL STRUCTURE OF A CONSTRUCTED CORDGRASS MARSH

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Abstract. Because tall vegetation can enhance habitat quality in intertidal wetlands, we examined the effects of N fertilization on the height growth of a constructed cordgrass (*Spartina foliosa*) marsh in San Diego Bay, where plants are short and soil N low. We varied the duration (therefore also the quantity; 30 g N/m^2 every month for 1, 2, 4, or 6 mo) and timing (30 g N/m^2 in March, April, June, or August) of N additions during 1993. By fertilizing a second set of replicates for the 6-mo treatment during 1994, we were able to examine the persistence of effects from 1993 vs. the effects of amendments in both years. Traditional canopy response measures (total stem length, maximum height, foliar N) increased most with the greatest duration/quantity of additions in 1993. All duration and timing treatments produced canopies with >100 stems/m^2 and ≥30 stems/m^2 taller than 90 cm, considered suitable for nesting by the endangered Light-footed Clapper Rail (*Rallus longirostris levipes*). However, without additional fertilizer in 1994, the previous year's canopy responses were not retained, suggesting insufficient storage of N in belowground tissues. Only plots fertilized in both years continued to produce ≥30 tall stems/m^2. The coarse dredge-spoil sediments of the constructed marsh had only 1/4 to 1/3 the total N found in the fine-textured soils of a nearby natural marsh, where cordgrass grows tall and clapper rails nest. We recommend that future marsh restoration projects begin with fine soils that promote N retention and accumulation to sustain tall canopies, rather than suggesting long-term fertilization.

Key words: California; canopy; cordgrass; endangered; fertilization; habitat; marsh; nitrogen; restoration; Spartina; *structure; wetlands.*

INTRODUCTION

Vertical structure of vegetation can be important to both arthropod (Turnbull 1960, Enders 1974, Uetz 1975, 1976, Denno 1980, Stiling 1980, Denno et al. 1981, Morris 1981, Samu et al. 1996) and avian (MacArthur and MacArthur 1961, Willson 1974, Bukacinska and Bukacinski 1993) species. Brown (1991) suggests that ''a more complex plant or plant community will provide a greater diversity of structures for feeding, overwintering, resting and basking, sexual display, and oviposition'' and that taller vegetation can accommodate more users and increase the probability of population survival and persistence. In coastal salt marshes, daily tides inundate the shorter plant stems of the low intertidal zone and some arthropods and birds require refuge from the highest seasonal tides and river flooding. Many marsh insects are neither adapted to immersion nor equipped to escape submergence through flight or movement on the surface film (Davis and Gray 1966). Stiling and Strong (1982) found that inundation can interrupt a parasitoid wasp's search for a host; consequently, parasitism is lower on leaves that are more

often submerged. Vince et al. (1981) found one grasshopper species to move up *S. alterniflora* stems with the rising tide, while a mirid species was most abundant high in the canopy. Ability to fly does not necessarily spare insects from flood tides; several salt marsh beetle species fall easily and drown as tidal waters rise (Davis and Gray 1966). Newly emerged or molted insects can risk damage by saltwater inundation before their cuticles become hard and waterproof (e.g., aphids [Foster and Treherne 1976]), suggesting that a tall-canopy refuge from tidal submergence is important. Similarly, birds that nest in low intertidal marshes risk inundation of nests and mortality of eggs and nestlings during the highest tides or river floods (Post 1974).

In southern California, tall cordgrass (*Spartina foliosa*) is important to salt marsh animals that are sensitive to tidal inundation. The light-footed clapper rail (*Rallus longirostris levipes*) has received the most attention because of its status as a federal- and state-listed endangered species. The rail lives and forages in stands of cordgrass, constructs its nest of dead cordgrass stems, and uses tall, live cordgrass for nest support and concealment (Massey et al. 1984). Tall cordgrass ensures that the rising tide water does not displace the floating nest (Massey et al. 1984). Also, a native coccinellid beetle (*Coleomegilla fuscilabris*) withstands high tides by moving to the tallest cordgrass plants (Williams 1990). *C. fuscilabris* is a major pred-

TABLE 1. Nitrogen addition studies on *Spartina alterniflora* on the U.S. East and Gulf of Mexico coasts.

Nitrogen addition study	Location	Natural (Nat.) or constructed (Con.)	Rate (g N/m²)	Frequency/duration
Sullivan and Daiber 1974	Delaware	Nat.	20	1×/mo for 12 mo
Broome et al. 1975	North Carolina	Nat.	5.6, 11.2, or 22.4	3×/yr (May–July) for 2 yr
		Con. (seedlings)	11.2	twice (June and July)
		Con. (transplants)	5.6, 11.2, or 22.4	once (Dec?)
Gallagher 1975	Georgia	Nat.	20	once (July)
Patrick and DeLaune 1976	Louisiana	Nat.	20	once (May)
Chalmers 1979	Georgia	Nat.	4	2×/mo for 12 mo
Valiela et al. 1985†	Massachusetts	Nat.	1.6, 5, or 15	2×/mo (Mar–Nov) for 12 yr
Osgood and Zieman 1993	Virginia	Nat.	127	once (April)

† See also Valiela et al. 1973, 1975, 1976, 1978; Valiela and Teal 1974; Vince et al. 1976, 1981.

ator of the armored scale insect *Haliaspis spartina,* which attaches and feeds on the adaxial surface of cordgrass blades. This native scale is never abundant in natural marshes where the cordgrass is tall, but it can reach outbreak densities where cordgrass stems are short (Boyer and Zedler 1996) and beetle densities are low (Williams 1989).

Like the other constructed marshes of San Diego Bay, Connector Marsh has shorter cordgrass canopies (Zedler 1993) and higher scale insect abundance than nearby natural marshes (Boyer and Zedler 1996). Although clapper rails consistently nest at the natural sites (Zembal et al. 1995), they have not used the constructed marshes. Short canopies appear to relate to the inadequate development of soil nitrogen (N), the concentration of which remains less than one-half that of natural marshes (J. B. Zedler and J. C. Callaway, *unpublished manuscript*). Soil N is correlated with organic carbon levels, which are also only about half that of natural levels (Cantilli 1989, Langis et al. 1991). Without adequate N, short cordgrass has little opportunity to become tall enough to attract either clapper rails or the predatory beetle that helps check scale herbivory. Locally, in natural marshes at Tijuana Estuary, both foliar N concentrations and biomass of cordgrass increased following addition of urea (46% N by mass), every 2 wk (Covin and Zedler 1988, Zedler et al. 1992). One-time additions of urea in a newly constructed marsh at San Diego Bay increased cordgrass heights, although not to reference marsh levels (Gibson et al. 1994), suggesting that a greater quantity or duration of N addition might achieve a greater height growth effect.

Of the many fertilization studies performed on another cordgrass species, *Spartina alterniflora,* on the U.S. Atlantic and Gulf of Mexico coasts (Table 1), only one examined the effects of fertilization in constructed marshes (Broome et al. 1975). Seedlings were fertilized at one constructed site, and transplanted culms at another; N addition increased biomass over controls (Broome et al. 1975). Half of the fertilization studies on naturally occurring *S. alterniflora* examined the

growth response to one-time additions of N (0.8–127 g N/m²), while the others used multiple applications over time (annual quantities of ~67–270 g N/m², Table 1). Osgood and Zieman (1993) reported significant increases in mean height and the other studies all found increased biomass after N fertilization, although Valiela et al. (1985) did not find a biomass response to their two lower doses until the second year. None of the previous studies varied the period of time over which N was applied during the growing season or the timing of additions. A study in Stiffkey, Norfolk, UK addressed the timing of N additions in salt marshes, but did not include *Spartina* (Jefferies and Perkins 1977).

This study examines the utility of nitrogen additions for increasing the height of *Spartina foliosa* (hereafter called simply ''cordgrass'') in Connector Marsh. Our goal was to determine which of a suite of N-addition treatments might produce cordgrass canopies as tall as those in natural marshes. We hypothesized that frequency, duration, and timing of N applications might each influence the cordgrass canopy response. We proposed several N-addition regimes during a single growing season, predicting that the longest duration of N additions would produce the greatest cordgrass response, but that a shorter duration of additions at the right time might suffice. The period of maximum growth for cordgrass is March–June (Winfield 1980), which is well after the period of winter storms and runoff. Unlike the precipitation and freshwater inflow regimes of the eastern U.S., which contribute N to the marshes throughout the year (Valiela and Teal 1979), nearly all precipitation in southern California occurs between November and March, and large storms are often accompanied by runoff that is high in nutrients. N can be especially limiting during the late-summer months when allochthonous N inputs are low. Because of seasonal differences in N supply and demand, we predicted a differential response to short-term additions at different times during the growing season, and expected the greatest response to result from late-summer fertilization.

We initially planned a one-year experiment, hypothesizing that canopies enhanced by N additions in 1993 would be sustained in 1994 through the accumulation of inorganic N in the soils, remineralization of N from dead organic material, or storage in belowground tissue followed by translocation to new shoots. Later, we asked if 1 yr of N addition would suffice, and we repeated the longest duration treatment (for which we had a duplicate set of plots) in a second growing season (1994). Nothing is known of N recycling and retention by *S. foliosa,* but White and Howes (1994) found that recycling of N (translocation + remineralization) plays a major role in the annual supply of N to the short form of *S. alterniflora,* meeting ~75% of the grass's annual N demand. We sought to understand the canopy response of *S. foliosa* to N additions within a single growing season and, by extending the experiment a second year, were able to examine the persistence of fertilization effects vs. the effects of multiyear amendments.

METHODS

Study location

Sweetwater Marsh National Wildlife Refuge (hereafter called the Refuge), 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 includes the largest remaining wetlands in San Diego Bay. Most of the wetland is intertidal salt marsh, with both natural and constructed areas. The marshes are tidally inundated in a mixed semidiurnal pattern (one tidal cycle is more extreme than the other each day) with a maximum spring tide range of 3 m.

This study focused on cordgrass-dominated low intertidal areas (elevation 0.3–0.6 m NGVD [U.S. National Geodetic Vertical Datum]) of Connector Marsh, a 4.9-ha wetland created to mitigate for damages during highway and flood control channel construction (Fig. 1). Connector Marsh is a series of islands and tidal channels excavated from dredge spoil in 1984 and planted with salt marsh vegetation in 1985. The north (2.1 ha) and south (2.8 ha) portions of Connector Marsh were each intended to support one breeding pair of light-footed clapper rails (DeWald and Rieger 1982). Both the north and south Connector Marsh receive tidal flows from the flood control channel, while the south portion also receives minimal tidal flows from the Sweetwater River. Sediments derived from the dredge spoil are coarse, ranging from loam to sandy loam (Swift 1988), with ~2.5% organic matter in 1990 (Pacific Estuarine Research Laboratory, *unpublished data*).

Paradise Creek, a 10-ha intertidal marsh adjacent to the constructed marsh, was used as a reference site for this study (Fig. 1). Sediments were characterized as clay loam in 1987 (Swift 1988) and had ~6.5% organic matter in 1990 (Pacific Estuarine Research Laboratory, *unpublished data*).
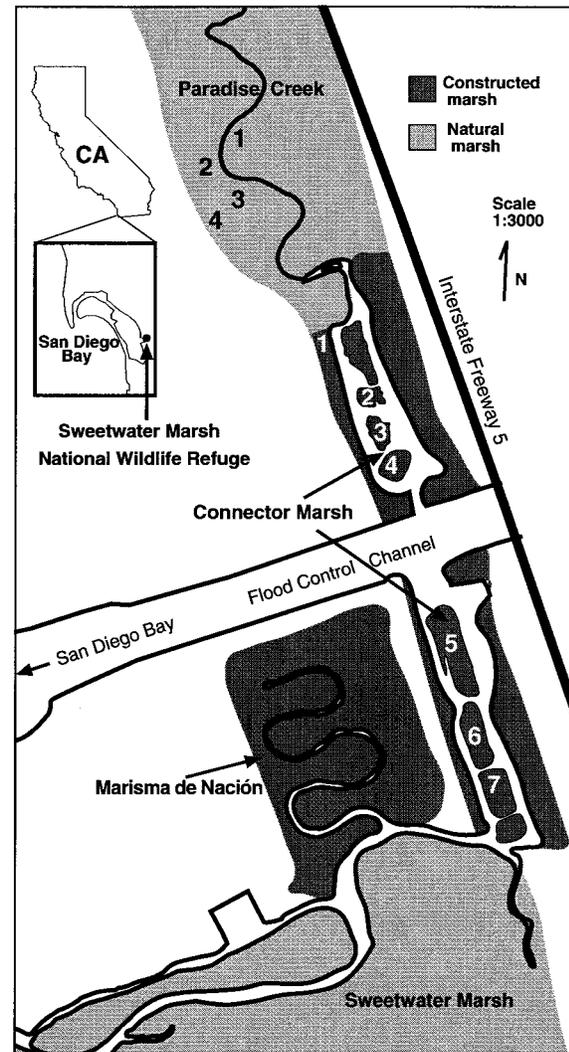

FIG. 1. Location of study at Sweetwater Marsh National Wildlife Refuge, San Diego Bay, San Diego, California. There were four experimental blocks in the natural marsh (Paradise Creek) and seven blocks in the constructed Connector Marsh.

Experimental treatments

In late February 1993, we set up a field experiment in pure cordgrass stands along channels in Connector Marsh using a randomized complete block design. Blocks were set up to account for a possible gradient in inundation time and flow rates (which could affect nutrient and salinity levels, sediment deposition, etc.), and treatments were randomly assigned within blocks. Fertilizer applications varied in duration/quantity (ranging from 1 to 6 mo during the 1993 growing season, a total of 30–180 g N/m^2) and timing (1-mo treatments in March, April, June, or August 1993, each totaling 30 g N/m^2)(Fig. 2). Treatment plots were 2 × 2 m with 2-m buffers between plots. Dead plant material was cleared from an additional control and a 6-

Total N added (g/m²)	Period of N application											Marsh	
	1993						1994					CM	PC
	March	April	May	June	July	August	March	April	May	June	July		
0												√	√
30	▆											√	
30		▆										√	
30				▆								√	
30						▆						√	
60	▆▆▆											√	
120	▆▆▆▆▆											√	
180	▆▆▆▆▆▆▆											√	√
180+150	▆▆▆▆▆▆▆						▆▆▆▆▆					√	

FIG. 2. Fertilization treatments, with bars representing duration of N additions in Connector Marsh (CM) and Paradise Creek (PC). Urea fertilizer (15 g N/m²) was applied every 2 wk at low tide for a range of durations and times.

mo treatment in Connector Marsh in February 1993 to investigate the effects of reducing a ''founder'' source of scale insects in a related experiment. We found no effect of this clearing on insect population growth (Boyer and Zedler 1996), nor was it expected to affect plant growth, so these treatments were pooled with their uncleared counterparts for analysis in 1993. In the second set of 6-mo treatment plots, amendments were repeated over a second growing season in 1994 (10 applications over 5 mo; Fig. 2).

At Paradise Creek Marsh, the control and the 6-mo treatment were performed in 1993, with 4-fold replication. We used fewer blocks and treatments in the natural marsh to reduce disturbance to the endangered Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*), which nested in the neighboring marsh plain. No additional fertilization was performed at Paradise Creek in 1994.

Urea fertilizer $(CO(NH_2)_2)$ was broadcast at a rate of 15 g N/m² every 2 wk, beginning in mid-March and continuing until September in 1993 and August in 1994. This application rate was comparable to that used by researchers on *Spartina alterniflora* (Table 1), although it was at the high end of the range for multiple application experiments. Our application rate was also high compared to the 5.2–10.4 g N/m² applied every 2 wk in natural *S. foliosa* marshes by Covin and Zedler (1988) and Johnson (1991). We chose to apply a greater quantity because of the high leaching rates of sandy soils in a nearby constructed marsh (Gibson et al. 1994). There were several reasons for our selection of urea instead of a mixed fertilizer: N is the primary nutrient found to limit *S. alterniflora* growth (Sullivan and Daiber 1974, Valiela and Teal 1974, Osgood and Zieman 1993, and others); *S. foliosa* was known to respond strongly to urea (Covin and Zedler 1988, Gibson et al. 1994); omitting other nutrients would allow for isolation of the N effect; and urea is inexpensive and readily available.

Response variables

Characteristics of soil (TKN, KCl-extractable N, salinity, and pH) and cordgrass (stem densities, heights, and foliar N) were measured monthly from March until September 1993 and in August 1994. Four randomly selected sediment cores (2.5 cm diameter by 15 cm depth) were taken from each plot, outside of the center 0.10-m² quadrat. Cores were composited, dried to a constant mass, ground with a mortar and pestle, and analyzed for total Kjeldahl nitrogen (TKN) (Quick-Chem Method 13-107-06-2-D), and KCl-extractable N (American Public Health Association 1992) using a Lachat autoanalyzer (Model No. 2100-000). Due to extremely low values of $[NO_3^- + NO_2^-]$ relative to NH_4^+, the NO_x data were not used. Nitrate is generally scarce in salt marshes (Kaplan et al. 1977, 1979, Lindau and Hossner 1981).

For pH and salinity, saturated soil pastes were made using standard methods (Richards 1954). To measure salinity in each sample, a drop of soil water was expressed through filter paper onto a temperature-compensated refractometer (Leica model No. 10419, VWR Scientific, Cerritos, California) using a 10-cm³ plastic syringe. Soil pH was measured using a pH meter and a combination electrode (model No. 34100-674, VWR Scientific).

Cordgrass heights were measured from the sediment surface to the tip of the longest leaf. We evaluated height distributions and judged whether cordgrass canopies were suitable for nesting by the light-footed clapper rail using the criteria of Zedler (1993), who proposed minimum density and height standards (≥100 stems/m² with ≥90 stems/m² over 60 cm tall, of which ≥30 stems/m² are over 90 cm in height) based on data for vegetation used for nesting by this bird.

Cordgrass heights were summed for each 0.10-m² quadrat to determine total stem length (TSL), a nondestructive method of estimating biomass (Zedler 1983), and the maximum height and stem density per quadrat were measured. Four stems per 2 × 2-m treatment plot were randomly selected for foliar N measures in May, July, and September 1993 and August 1994 (in all seven blocks in May 1993 and August 1994, and in four blocks in July and September 1993); no stems were removed from the center 0.10 m². Leaf

tissue was rinsed, dried at 60°C to a constant mass, and ground with a Wiley mill. TKN was estimated for the leaf tissue using the methods described in the first paragraph of this section.

We determined the total fiber and lignin content of the cordgrass tissue collected in September 1993 to see if the tough plant tissues observed in the field were due to N addition. A sequential fiber analysis (procedure from Goering and Van Soest 1970, modified by Van Soest and Robertson 1985) was performed on the ground leaf tissue collected in September 1993 and described above. First, a neutral detergent fiber hydrolysis removed cell soluble components from the sample, leaving hemicellulose, cellulose, lignin, and any undissolved minerals. Acid detergent fiber hydrolysis, then acid hydrolysis, removed hemicellulose and cellulose, respectively, leaving lignin. Ashing removed lignin from the sample, leaving behind only undissolved materials.

Statistical analyses

The Kolmogorov-Smirnov two-tailed test for large sample sizes was used to compare the distributions of cordgrass stem heights at the end of each growing season. Two-way analysis of variance (ANOVA) was used to test for block and treatment effects on soil (TKN, NH_4^+, salinity, and pH) and canopy responses (stem density, TSL, and foliar N) for each sampling date. In the same manner, fiber content was analyzed for the September 1993 data, and maximum stem height and standing crop of N were examined for the late-season data in both years. Because of the varied timing and duration of fertilization, some of the 1993 treatments were not complete until September. For analyses prior to September, values for equivalent treatments were pooled (e.g., all treatments that had not yet received any N additions were pooled with the controls), and the two 6-mo treatments were also pooled. Significance levels were set at $\alpha = 0.05$ for all tests. Residuals were examined and data were transformed when necessary to improve homoscedasticity (log transformations on foliar N, TSL, and soil salinity; $\log[x + 1]$ on soil TKN and NH_4^+ data).

The Tukey hsd method (=T method) was used for multiple comparisons (Tukey 1953), and when sample sizes were unequal due to pooling, the Tukey-Kramer method was used (Day and Quinn 1989). The statistics programs SYSTAT (SYSTAT 1992) and SuperANOVA (Abacus Concepts 1991) were used.

RESULTS AND DISCUSSION

Soils in Year 1

In 1993, there were no significant effects of fertilization on soil TKN or NH_4^+ in Connector Marsh, even where plots were fertilized for 6 mo (Fig. 3). TKN in Connector Marsh was generally less than one-third that of Paradise Creek Marsh, even with the greatest urea
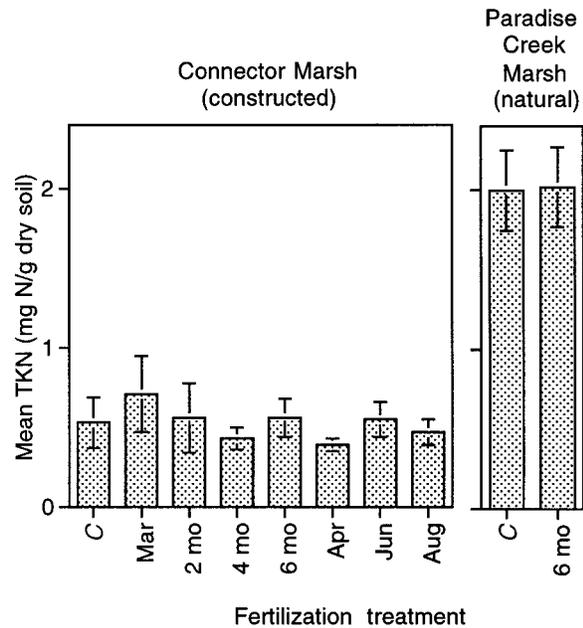

FIG. 3. Mean total Kjeldahl nitrogen (TKN) by treatment in Connector Marsh ($n = 7$) and Paradise Creek ($n = 4$), September 1993. C = control (unfertilized) treatment. Error bars represent ± 1 SE. Nitrogen is per gram dry mass of soil.

application (0.56 $\pm$ 0.12 and 2.02 $\pm$ 0.25 mg/g, respectively, in September 1993; Fig. 3). As with TKN, even maximum fertilization failed to bring NH_4^+ values in Connector Marsh (6.49 $\pm$ 1.34 μg/g) to Paradise Creek levels (21.31 $\pm$ 9.31 μg/g) by September 1993. This suggests that N retention was poor in the constructed-marsh soils, or that uptake by plants was high, as expected in a N-limited system that is supplied N. In Connector Marsh, the most northerly block (Fig. 1) was highest in soil NH_4^+ and TKN in nearly all months in 1993 (ANOVA, P always < 0.01; Tukey-Kramer test, P always < 0.05). This block occurred in an area that tended to be waterlogged even during the lowest tides, possibly affecting uptake of N by cordgrass; waterlogging has been shown to impact *S. alterniflora* negatively (Linthurst and Seneca 1980, Mendelssohn and Seneca 1980, Howes et al. 1981), through anoxia, increased sulfide levels, and inhibition of NH_4^+ uptake (Koch et al. 1990).

In Paradise Creek Marsh, neither total N or NH_4^+ increased over the 6-mo period of fertilization relative to controls. High soil N levels (Fig. 3) suggest that the cordgrass in this natural marsh is not as limited by N, but uptake by plants is still a possible fate of the added N.

Soil pH was not reduced by fertilization in 1993 in either the constructed or natural marsh (ANOVAs, P > 0.05), as can occur with NH_4^+ fertilizers (Singer and Munns 1987, Tisdale et al. 1985). There was a seasonal increase of ~1 pH unit in both marshes; however, it was unrelated to N addition (pH in control plots from March to September: 6.7 $\pm$ 0.1 to 7.6 $\pm$ 0.1 in Con-
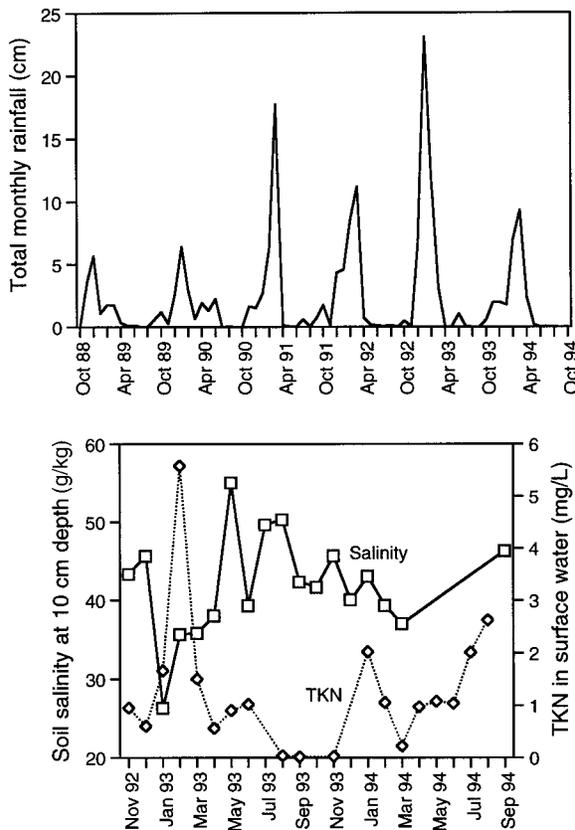
FIG. 4.   Temporal changes in rainfall, soil salinity (at north end of Connector Marsh), and total Kjeldahl nitrogen (TKN) of channel surface water (at the north end of Paradise Creek). Rainfall data are from San Diego Lindbergh Field; salinity and TKN are from Pacific Estuarine Research Laboratory's long-term monitoring program. Note the decrease in soil salinity and the increase in channel water N with heavy rainfall and flooding in early 1993.

nector Marsh and 6.3 ± 0.1 to 7.4 ± 0.1 in Paradise Creek). Soil salinity did not increase with N addition (ANOVAs, $P > 0.05$), in contrast with Chalmers' (1979) findings in *S. alterniflora* experimental plots in Georgia. A seasonal increase in soil salinity occurred in both marshes between April and September 1993, a period with only ~1 cm of precipitation (San Diego Lindbergh Field data;[2] see Fig. 4). In the Connector Marsh control plots, mean soil salinity increased from 25 ± 3.1 to 40 ± 3.3 g/kg during the growing season, and in Paradise Creek from 38 ± 5.5 to 66 ± 7.9 g/kg for the same period. In East Coast marshes, *S. alterniflora* growth can be inhibited at concentrations of 40 g/kg (Haines and Dunn 1976) and 45 g/kg (Woodhouse et al. 1972); however, salt marshes in our region are commonly hypersaline due to low rainfall, and these levels are within the range previously found (Zedler 1983).

Canopy response in Year 1

Varied duration of N additions.—Height distributions were compared to the criteria for clapper rail nesting suggested by Zedler (1993), i.e., density of ≥ 100 stems/m^2 with ≥ 30 stems/m^2 taller than 90 cm. By August and September 1993, all of the fertilization treatments met these canopy height criteria, while the control did not (Fig. 5). More tall stems occurred in fertilized plots than in the control, even with only 1 mo of amendments (Fig. 5; Kolmogorov-Smirnov test on mean of March, April, and June treatments, $D = 15.7 > D_a = 12.9$). The cumulative frequency curve for the control plots has a steep initial slope indicative of a large percentage of short stems (there were no stems >90 cm), while the curves for the N-amended plots are S-shaped and initially flatter, with the number of taller stems increasing in proportion to the amount of N added (Fig. 5). Connector Marsh plots fertilized for 4 or 6 mo achieved height distributions similar to those of controls at Paradise Creek Marsh, as evidenced by overlapping cumulative percent frequency plots (Fig. 5). These treatment plots in Connector Marsh had some stems >120 cm tall.

In August and September, maximum stem height ranked according to the amount of N applied in Connector Marsh. In September, maximum stem height in the control (81 ± 5.8 cm) was significantly lower than the 2- (104 ± 2.1 cm), 4- (110 ± 3.7 cm), and 6-mo treatments (111 ± 5.3 cm) (ANOVA, $P = 0.0001$; Tukey-Kramer test, $P < 0.05$). Fertilized cordgrass was comparable to Paradise Creek Marsh maximum heights (114 ± 9.7 cm in the control and 120 ± 9.2 cm in the 6-mo treatment plots).

Effects of fertilization on TSL were noticeable as early as May, when plots that had been fertilized for only 2 mo (March and April) exceeded the controls (Fig. 6; ANOVA, $P = 0.003$; Tukey-Kramer test, $P < 0.05$). The longest duration treatments were always significantly greater than the controls from May through September (Fig. 6; ANOVA, P always < 0.05). Late in the season (August and September), the 6- and 4-mo treatments had the highest TSL (300 ± 35 m/m^2 and 276 ± 19 m/m^2, respectively, in September), followed by the 2-mo treatment (220 ± 24 m/m^2), while the control was lower than all three (131 ± 22 m/m^2; ANOVA, $P = 0.0001$ in both months; Tukey-Kramer test, $P < 0.05$). Both the 6- and 4-mo treatments increased TSL in Connector Marsh to levels comparable to the natural marsh, Paradise Creek (September grand mean including fertilized treatment and controls = 246 $\pm$ 36 m/m^2).

Mean foliar N differed significantly by treatment in Connector Marsh for all 3 mo analyzed: May, July, and September (two-way ANOVA, $P = 0.0001$ for all months). In all cases, mean foliar N was higher with maximum fertilization than in the control (Tukey-Kramer test, $P < 0.05$). In September, foliar N in the con-
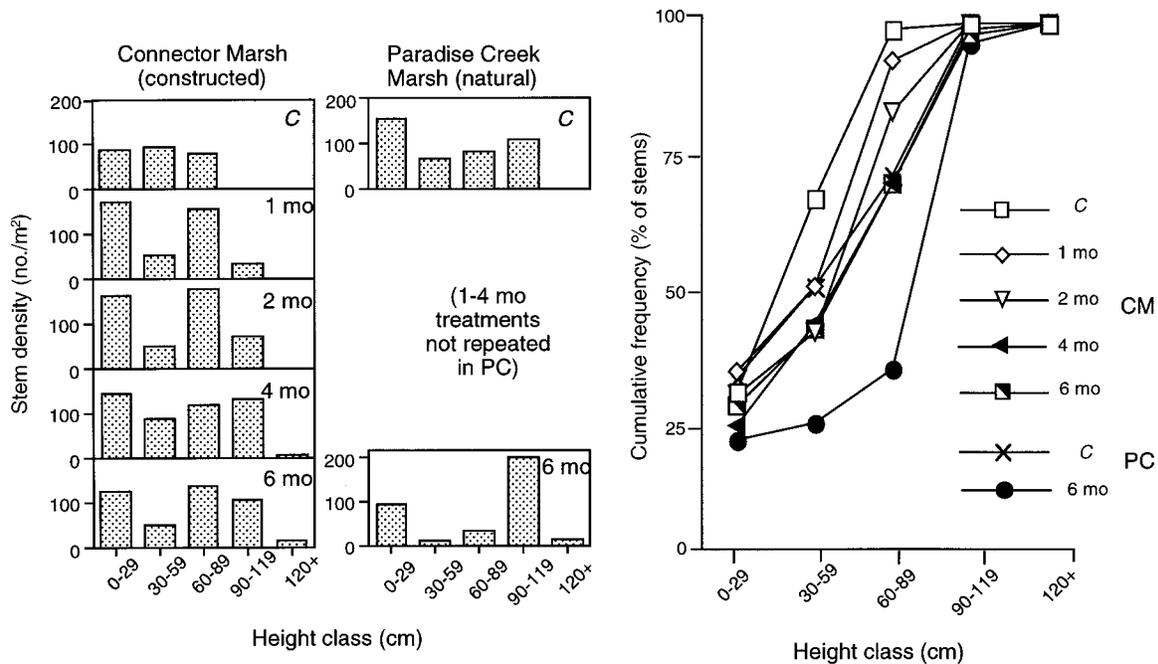
FIG. 5. Fertilization effects on number of stems/m² and cumulative frequency (percentage) in 30-cm height classes, Connector Marsh and Paradise Creek, September 1993. All fertilization treatments in Connector Marsh met cordgrass height criteria for Light-footed Clapper Rail nesting (at least 30 stems/m² >90 cm), while the control (C) did not. The cumulative percent frequency plot shows that 4 or 6 mo of N additions in Connector Marsh resulted in height distributions similar to Paradise Creek Marsh controls, and that N additions in Paradise Creek produced even more very tall stems.

trol averaged 13.9 ± 0.8 mg N/g and in the 6-mo treatment it averaged 19.0 ± 0.6 mg N/g.

At the end of the season (September), aboveground standing crop of N (foliar N as a percentage of dry mass × dry biomass, the latter estimated from TSL), was significantly higher in the 6-mo treatment plots (48.3 ± 4.8 g N/m²) than in the control (12.8 ± 1.79 g N/m²), as were the 4-mo and April treatments (Fig. 7; ANOVA, $P = 0.0001$; Tukey-Kramer test, $P < 0.05$). With maximum fertilization, levels of foliar N and aboveground N standing crop (Fig. 7) were comparable to natural marsh levels. Aboveground standing N crop was high relative to a nearby constructed marsh (Marisma de Nación) where Gibson et al. (1994) found <2 g N/m² in aboveground tissue after a one-time addition of 107 g N/m²; they attributed this poor response to high decomposition and leaching rates in the sandy soils. Our greatest N-addition treatment (180 g N/m² over 6 mo) produced a response nearly 25× greater than the one-time N addition of Gibson et al. (1994), and even our control plots averaged >5× the aboveground standing crop of N in their study. The greater biomass of the constructed marsh in the current study may relate to its greater age (planted in 1985). The previous study concerned cordgrass planted at a bare site (Gibson et al. 1994), where shoot densities increased with N addition in the first year (Gibson et al. 1994). In the present study, cordgrass had developed

high shoot densities before N addition, and height growth was the main response.

From 20 to 60% of the N we added was recovered by aboveground tissue in Connector Marsh in 1993 (Fig. 7). N was incorporated most effectively with single-month additions in April, June, and August (30 g N/m² added, ~45–60% recovered = 13.5–18 g N/m²). This is 2–5× the amount of N recovered in fertilized *S. alterniflora* marshes (Broome et al. 1975, Patrick and DeLaune 1976). Our longer additions all had similar recovery rates of 20–25% by aerial tissues (60–180 g N/m² added, ~12–36 g N/m² recovered, respectively). In comparison, the recovery of N in Paradise Creek Marsh was only 7% (180 g N/m² added, 13 g N/m² recovered) after 6 mo of urea additions, suggesting there was lower N demand or that something else limited N uptake.

By September 1993, cordgrass density had exceeded 400 stems/m² in both Connector Marsh and Paradise Creek (grand means including fertilized plots and controls). Unlike the other growth response variables, mean stem density differed by treatment only in June ($P = 0.048$), when the control had the fewest stems (247 ± 30 stems/m²) and the longest duration treatment (3 mo at that time) had the most (340 ± 35 stems/m²). Increased biomass after fertilizer addition was not accompanied by a reduction in stem density, in contrast with studies of *Spartina alterniflora* in Massachusetts (Valiela et al. 1978; see also Vince et al. 1976).
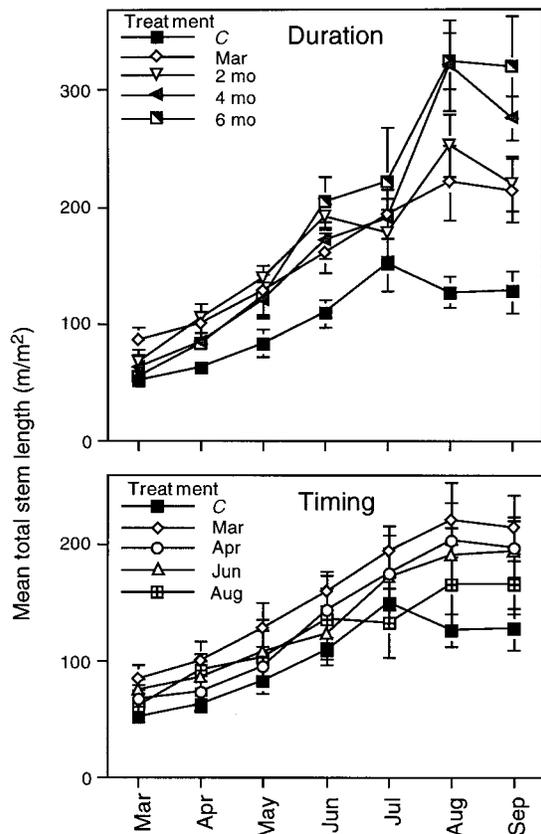
FIG. 6. Mean TSL in Connector Marsh, March–September 1993. Four durations of N additions and four single-month pulses of N at different times are compared to the control. *C* = control (unfertilized) treatment. Error bars represent ±1 SE; *n* = 7.
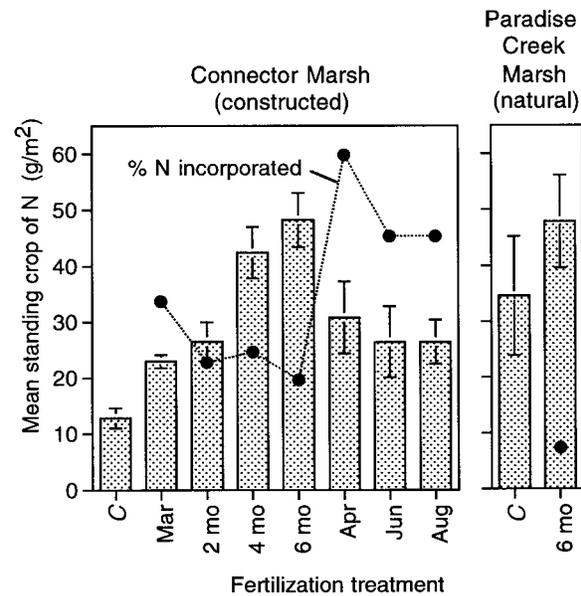

FIG. 7. Mean standing N crop (aboveground biomass times foliar N concentration) and percentage N incorporated by treatment in Connector Marsh (*n* = 7) and Paradise Creek (*n* = 4), September 1993. *C* = control (unfertilized) treatment. Error bars represent ±1 SE. Total N added was 30, 60, 120, and 180 g/m² for the 1-, 2-, 4-, and 6-mo treatments, respectively.

Our field observations led us to suspect that fertilizing throughout the 1993 growing season "toughened" cordgrass tissues. Stems and blades appeared stiffer and tougher in plots where the most fertilizer was applied. However, there were no significant differences in total fiber or lignin in the leaf tissues of the control and 6-mo treatments (22.0 ± 0.8 vs. 20.9 ± 0.4% for fiber and 1.0 ± 0.7 vs. 1.6 ± 0.3% for lignin in the control and 6-mo treatment, respectively), nor did Paradise Creek Marsh differ from Connector Marsh (ANOVA, *P* > 0.05).

Short-term N additions at different times.—Short-term N additions had a lesser effect on the plant canopy but still produced cordgrass tall enough to meet clapper rail nesting criteria (>30 stems over 90 cm) in 1993. Identifying the best time for a short-term N pulse proved complex, as results differed for different response variables. When compared to the controls in September 1993, both the March and June treatments had significantly taller maximum height, the March treatment was greater in TSL, and the April treatment had greater N standing crop (ANOVA, *P* always = 0.0001; Tukey-Kramer test, *P* < 0.05).

In general, the single-month fertilizer treatments increased foliar N in the month following N addition, but differences were not detected later. For example, plots fertilized only in April had higher foliar N than the controls when sampled in May (ANOVA, *P* = 0.0001; Tukey-Kramer test, *P* < 0.05) but were similar to controls by July. For each of the March, April, and June treatments, foliar N returned to control levels within 2 mo, but treatment effects were reflected in growth differences when sampled in September 1993 (described above). The August-fertilized plots exceeded foliar N levels of the controls when sampled in September (ANOVA, *P* = 0.0001; Tukey-Kramer test, *P* < 0.05) and matched N levels of the longest duration treatment (6 mo); however, continued or delayed responses were not sampled in later months as we expected plant senescence to mask treatment effects.

When measured in September 1993, the April treatment plots had incorporated more of the added N into their aerial tissues (60%; Fig. 7) than the other single-month treatments (35% in March and 45% in June and August). This suggests that N demand was lowest in March, especially high in April, and intermediate in June and August. N inputs from winter storms were still relatively high in March but dropped in April (Fig. 4), possibly explaining the higher N demand in April.

These results do not support our hypothesis that short-term N additions during the late summer (when other N inputs are low) would produce a greater cordgrass response than additions at other times. In fact,

annual additions early in the growing season (April) might provide a N pulse more similar to the winter/spring nutrient inputs to which this system is adapted, while reducing disturbances associated with continued amendments throughout the growing season.

Natural marsh response.—The higher soil N levels in Paradise Creek Marsh (~3× greater than Connector Marsh) suggest that cordgrass in the natural marsh has more N potentially available to plants than the constructed marsh. Greater TSL, more plants in the tallest height classes, and greater standing N crop support this hypothesis. In addition, fertilized plants in the natural marsh incorporated a relatively low percentage of N into aboveground tissues (7 vs. 20% for the same treatment in Connector Marsh; Fig. 7), and there was no fertilization response in foliar N, TSL, maximum height, or stem density. But despite the lack of response found by the other measures, a shift in Paradise Creek stem height distributions occurred, with an even greater proportion of the tallest stems produced than occur naturally (control distribution significantly different than fertilized: Kolmogorov-Smirnov test, $D = 34.1 > D_a = 17.0$; Fig. 5). Overall, these findings suggest that this natural marsh is less limited by N than Connector Marsh.

Paradise Creek marsh may also be less limited by N than the nearby natural marshes at Tijuana Estuary. Studies there found increased foliar N and TSL with fertilization (Covin and Zedler 1988, Zedler et al. 1992). Cordgrass TSL at Tijuana Estuary (100 m/m²; Pacific Estuarine Research Laboratory 1993) has been lower than at the natural marshes at San Diego Bay due to lower stem density (160 stems/m²; Pacific Estuarine Research Laboratory 1993). Lower stem density and a significant biomass and tissue N response suggest greater N-limitation at Tijuana Estuary than at Paradise Creek Marsh. Nonetheless, Tijuana Estuary supports one of the largest populations of nesting rails in southern California (Jorgensen 1975, Zembal et al. 1995) with its large proportion of tall stems (Zedler 1993).

Soils in Year 2

When measured in August 1994, the treatment fertilized for a second growing season (March to August 1994) in Connector Marsh was similar in all soil factors to the plots fertilized only in 1993. Soil TKN averaged 0.78 ± 0.21 mg/g following fertilization in both years and 0.81 ± 0.15 mg/g without urea additions. As in 1993, constructed-marsh TKN levels were approximately one-third as high as in Paradise Creek Marsh (2.57 ± 0.16 mg/g in the control). Although rainfall and associated N inputs were lower in 1994 than 1993 (Fig. 4), soil TKN levels were similar in the two years within each marsh (even with N additions). Compared to a previous study of the same constructed and natural marshes (Langis et al. 1991), the difference in soil TKN appears to have widened. Although Connector Marsh
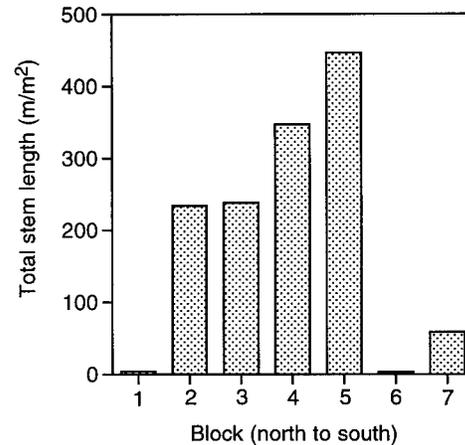

Fig. 8. Total stem length (TSL) by block for the treatment fertilized in both 1993 (for 6 mo) and 1994 (for 5 mo) in Connector Marsh, August 1994. Each bar represents TSL in one 0.10-m² quadrat, converted to 1-m² area.

levels are similar to those found in 1988 and 1989 (mean = 0.91 mg/g), Paradise Creek soil TKN has increased from the previous study (mean = 1.88 mg/g).

Soil NH_4^+ was similar for all treatments when measured in August 1994 in Connector Marsh, as it was in 1993. NH_4^+ levels were high in 1994; control plots averaged 15.16 ± 4.67 μg/g in 1994, compared to 4.77 ± 0.98 μg/g in September 1993. High NH_4^+ at Connector Marsh suggests that organic N was being mineralized to NH_4^+, increasing availability of N for plant uptake.

Soil pH did not differ by treatment in either Connector Marsh or Paradise Creek in August 1994; it was near circumneutral for all treatments. Similarly, soil salinity did not differ by treatment in either marsh. Soil salinity declined from late 1993 levels by ~9 g/kg (to 31 ± 2.6 g/kg) and 12 g/kg in Paradise Creek (to 54 ± 4.7 g/kg), despite lower rainfall in 1994 (Fig. 4) and similar average monthly temperatures among years (San Diego's Lindbergh Field data [see footnote 2, page 697]). Although this decrease is unexplained, these soil salinities are within the range of interannual variability found in these marshes (Zedler 1983; Pacific Estuarine Research Laboratory, *unpublished data*).

Canopy response in Year 2

Damage to cordgrass.—Our Year-2 treatment responses were complicated by canopy damage that was first detected in July 1994. Patches of dead cordgrass 1–6 m² in size and lesser damage in areas of 50–60 m² became apparent throughout the natural and constructed marshes. No treatments in Connector Marsh were exempt from damage. Three of the seven plots fertilized for two growing seasons were affected, and two had <5% of the TSL in the highest plot (Fig. 8). There were control and short-term fertilized plots that were damaged as badly as some of the two-season fertilized

TABLE 2. Coefficient of variation (n = seven 0.10-m^2 quadrats) for stem density and total stem length (TSL) by treatment in Connector Marsh, August 1994. All nitrogen treatments occurred in 1993 except for the last, which occurred in both 1993 (for 6 mo) and 1994 (for 5 mo).

Treatment	Coefficient of variation (%)	
	Stem density	TSL
C	38.2	27.5
Mar	49.7	37.9
2 mo	75.3	83.3
4 mo	50.0	60.0
6 mo	68.4	69.9
Apr	39.5	45.7
Jun	39.9	38.7
Aug	28.1	42.6
1993 + 1994	87.0	94.5

plots. Overall, the control plots were the least variable in TSL, and the two-season treatment plots were the most variable (Table 2), though the variability in the latter was exaggerated by the large growth response to fertilization in the undamaged plots within the treatment. Several factors may have contributed to the mortality of cordgrass, including wrack accumulation, small-mammal damage (evidenced by teeth marks along stem bases), and herbivory by lepidopteran larvae (*Thaumatopsis fieldellus* [T. Eichlin, California Department of Food and Agriculture, and B. Landry, University of California, Berkeley, California]), which were found boring and feeding within the lower 10–30 cm of cordgrass stems throughout the marshes.

Persistence of fertilizer effects from Year 1.—Al-

though little N was retained in Connector Marsh soils in 1993, we hypothesized that fertilized cordgrass might store N belowground and that translocation could stimulate growth in 1994. We predicted that the greatest response would occur where we applied the most fertilizer in 1993, but that some of the single-month treatments might also show a lasting response (e.g., the April treatment with its high N recovery measured in September 1993). However, in August 1994, none of the plots fertilized only in 1993 met Zedler's (1993) canopy height criteria (Fig. 9), nor did they differ from controls in maximum height, TSL (Fig. 10), foliar N, standing crop of N, or stem density. While they did not meet the canopy height criteria, two of the treatments from 1993 had stems >90 cm: 16 stems/m^2 in the 6-mo treatment and 9 stems/m^2 in the April treatment (indicating some lasting response of the high N recovery in 1993), while there were none in the controls or the other 1993 fertilizer treatments. Compared to controls, there was also a greater frequency of tall stems in the 61–90 cm class even with the lowest N addition rate (mean of 1-mo treatments; Kolmogorov-Smirnov $D = 28.4 > D_a = 12.5$). For example, with 6 mo of N additions in 1993, there were 66 more stems/m^2 in the 61–90 cm class than in controls when sampled in August 1994 (Fig. 9). Although the canopy height criteria for clapper rail nesting (Zedler 1993) did not continue to be met in 1994, these shifts in height distribution suggest that some fertilization effect persisted from the previous year.

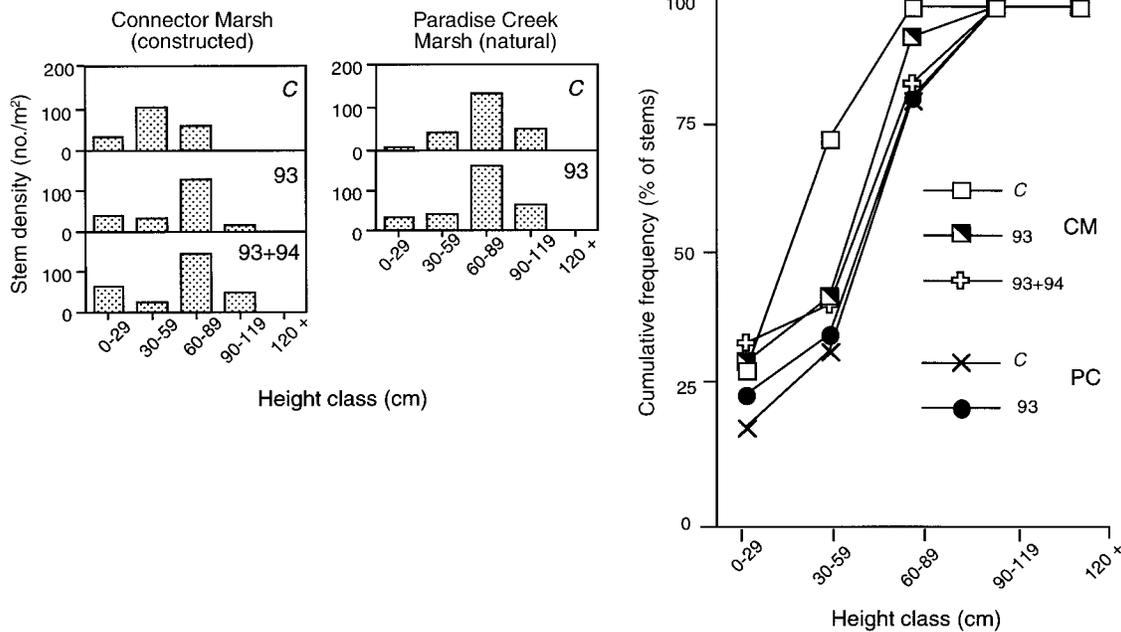In 1993, the natural marsh at Paradise Creek showed

FIG. 9. Number of stems/m^2 and cumulative frequency (percentage) in 30-cm height classes, Connector Marsh and Paradise Creek, August 1994. C = control (unfertilized) treatment. Only those plots fertilized in both 1993 (for 6 mo) and 1994 (for 5 mo) met cordgrass height criteria (≥30 stems/m^2 taller than 90 cm) in Connector Marsh at the end of Year 2, as shown by the similar cumulative frequency distributions.
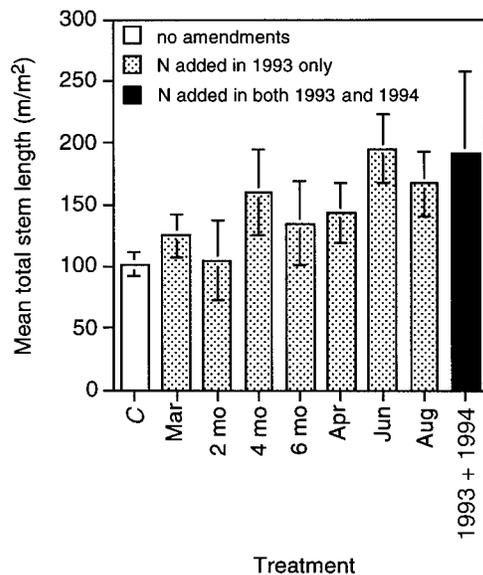
FIG. 10. Mean TSL in Connector Marsh in August 1994, after N additions during one or two growing seasons in $n =$ seven 0.10-m^2 quadrats. C = control (unfertilized) treatment. Error bars represent ±1 SE.

no evidence of a fertilization response in maximum height, TSL, foliar N, standing crop of N, or stem density in 1993; hence, it was not surprising that these measures did not differ in August 1994, as no N was added that year. Height distributions sampled in August 1994 did not differ between the controls and those plots fertilized only in Year 1 (Kolmogorov-Smirnov test, $D = 7.8 < D_a = 12.5$; Fig. 10), despite the increase in the number of tall stems (>90 cm) with fertilization found in September 1993 (Fig. 6).

Effects of N amendments over two growing seasons.—Only plots fertilized in both 1993 and 1994 had enough tall stems to meet the canopy height criteria for clapper rail nesting (Zedler 1993) at the end of the second growing season (Fig. 9). Foliar N was also significantly greater in the plots fertilized in both 1993 and 1994 (22.0 ± 0.9 mg N/g) than those fertilized in 1993 only (17.9 ± 1.4 mg N/g) or the controls (16.2 ± 0.7 mg N/g) (ANOVA, $P = 0.0001$; Tukey-Kramer test, $P < 0.05$), suggesting the potential for greater growth or N recycling with fertilization in both years. Plots fertilized the most in 1993 (6 and 4 mo) ranked behind plots that were fertilized in both years in foliar N levels, but did not differ from the other treatments or controls. No other vegetation measures (e.g., TSL, Fig. 10) differed between the controls, the plots fertilized in 1993, and those fertilized in both 1993 and 1994. Damages to cordgrass in some treatment plots (discussed above) may have masked differences in these more standard vegetation measures (as opposed to height histograms). For example, the low stem density and TSL in three out of seven plots in the 2-yr treatment resulted in high variability (Fig. 8), yet TSL

was 2–3× greater in the undamaged plots in this treatment (~230–450 m/m^2) than in the controls plots (maximum TSL = 131 m/m^2).

Implications for wetland restoration and management

Wetland animals are often the target for management efforts, and wetland restoration can hardly be judged successful if transplanted vegetation fails to support the fauna of reference wetlands. In southern California, tall cordgrass provides habitat for the light-footed clapper rail and the beetle *C. fuscilabris,* both of which prey on insect herbivores of cordgrass (Jorgensen 1975, Williams 1989, Johnson 1991). Higher abundances of predators could reduce herbivory damage and improve plant growth (Boyer and Zedler 1996). Yet the cordgrass at the constructed Connector Marsh is unlikely to provide habitat for these predator species; despite high shoot densities, plants remain short, even 10 yr after planting. Nitrogen fertilization during a single growing season (over 1, 2, 4, or 6 mo) increased heights so that canopies met standards for clapper rail nesting (Zedler 1993), but this response did not persist into a second year unless N continued to be added. Still, there was some sustained effect at the end of the 1994 growing season, as evidenced by more tall stems in plots fertilized only in 1993 than in control plots. Although there were not enough tall stems to meet the canopy height criteria for clapper rail nesting, this sustained difference in height distribution suggests that additional years of fertilization might promote further accumulation and recycling of N.

But how long might it take to develop N stores equivalent to natural marshes? Without fertilizer, Lindau and Hossner (1981) predicted that it would take 2–5 yr for constructed marshes to reach natural marsh levels of organic matter and nutrients in Texas, while in North Carolina, Craft et al. (1988) predicted 15–30 yr would be needed to reach natural marsh macroorganic matter N levels and "considerably longer" for soil N. Our natural marshes are more similar to those of Lindau and Hossner (1981), with relatively low organic matter (2–6%, Langis et al. 1991). Yet at 10 yr, Connector Marsh lagged well behind the predictions of Lindau and Hossner (1981) based on soil total N. If we were to select one of our treatments for use in accelerating the process of organic matter and N pool development, it would be the 6-mo addition of urea every 2 wk, which produced the greatest growth responses. We would need to determine how to translate our experimental methods to large areas of the marsh. The mitigation agreement for the constructed marshes at the Refuge requires that there be one large patch (90–100 m^2) of tall, dense cordgrass for each of seven potential "clapper rail home ranges" for a period of 3 yr (U.S. Fish and Wildlife Service Biological Opinion #1-1-78-F-14-R2 [U.S. Fish and Wildlife Service, 2730 Loker Avenue West, Carlsbad, California, USA]). To account for

patchy damage that occurs naturally (from wrack accumulation, herbivory, etc.), fertilizing areas >100 m^2 would be desirable.

With these assumptions in mind, we began a large-scale fertilizing program at Connector Marsh in 1995, selecting three areas of pure or nearly pure cordgrass, each ~400 m^2. We constructed a boardwalk system with trestles and movable planks to minimize trampling, and spread urea fertilizer every 2 wk during the growing season using a portable, hand-cranked spreader. However, by 1996, sediment had accumulated in some places (Haltiner et al. 1997), and this may have contributed to an observed shift in species composition at one fertilized patch (Boyer and Zedler, *in press*). By fall 1996, this patch had insufficient area of cordgrass to meet the mitigation criteria. Thus in 1997, we had to uproot the trestles and move the boardwalk to a new cordgrass patch, damaging the marsh in the process. With few patches of potentially tall cordgrass, and without knowing where sediments might accrete, we conclude that it would be difficult to produce and sustain seven large, tall patches of cordgrass with continual N fertilization. Furthermore, the mitigation requirement is to provide a *self-sustaining* tall canopy; if the locations of fertilizer addition must be moved repeatedly, the possibility of increasing N accumulation that might eventually lead to self-sustaining tall plants seems remote.

In view of the many constraints of long-term N addition in achieving tall vegetation, we do not support an ongoing fertilization program. Instead, we propose focusing on the source of the N-retention problem, i.e., sandy soils too low in organic matter to supply nutrients and too coarse in texture to retain nutrients. The use of fine, organic substrates at the time of marsh construction is likely to improve the ability of a new marsh to retain and accumulate the nutrients needed to sustain tall cordgrass canopies. We recommend salvaging wetland soils from sites that are undergoing development (e.g., highway widening, flood control channeling), and transplanting whole blocks of sod, complete with root and rhizome systems. When sod is not available, fine sediment should be imported. In sites with higher sedimentation rates, the marsh plain could be overexcavated, relying on accretion of fine materials to create the desired marsh substrate.

We further suggest an approach to creating clapper rail nesting habitat that recognizes the importance of creek and channel edges in supporting the tallest, densest cordgrass. Future projects should create habitat with a high density of tidal creeks and substantial edge between mudflat and marsh. At Tijuana Estuary, where >60 pairs of clapper rails consistently nest (1992–1995 data from Zembal et al. 1995), tidal creek density is high, with ~40% of the channel length being first-order (small, narrow) creeks (Desmond 1996).

Because every restoration project involves unknowns, we recommend that habitat construction be undertaken with an adaptive management approach (Nyden and Zedler 1996). Although Connector Marsh has not achieved the desired nesting habitat standards or attracted the target clapper rail, it does support many native plants and animals, including other endangered species. Thus, it is too late to modify this marsh by adding fine organic soils or cutting more tidal creeks. Such a project would be costly and damaging to the biota of the marsh. We do not recommend disturbing the existing habitat values. Instead, we suggest that additional wetland be excavated from the adjacent dredge spoil fill, using finer substrate and adding more tidal creeks.

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