

Evaluating the Progress of Restored Cordgrass (*Spartina foliosa*) Marshes: Belowground Biomass and Tissue Nitrogen

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ABSTRACT: We report the first data on belowground tissue mass and nitrogen (N) concentration for *Spartina foliosa* in southern California, assessing one natural and two constructed marshes on San Diego Bay. Biomass at the natural marsh was low compared to that of other *Spartina* spp., but higher than values reported for *S. foliosa* in northern California. In sandy constructed marshes planted 5 and 10 years before this study, *S. foliosa* had lower belowground tissue N, lower N crop (%N × biomass), and shallower roots than in the adjacent natural marsh. We took advantage of a 2-yr, large-scale fertilization project being performed in the older constructed marsh and examined biomass and N storage after N additions. Although there was a trend toward N accumulation with fertilization, N crop remained at approximately 50% of natural marsh levels, unlike the large aboveground responses to N addition in our previous studies. Lower belowground reserves help to explain poor aerial growth in the created marshes and suggest the need for finer sediments (with greater potential for holding and supplying nutrients) to sustain *S. foliosa*. While fine sediments are beginning to accumulate on the surface of the created marshes, vertical accretion is more likely to shift the plant community toward other species than to enhance *S. foliosa* growth. We suggest salvaging and importing fine, organic marsh sediments or providing organic amendments to establish proper substrate conditions. Overexcavating and allowing fine sediments to accumulate remains an option, although the time scale is unpredictable due to the stochasticity of accretion events.

Introduction

Stability and resilience of perennial vegetation are conferred in part by storage and recycling of carbon compounds and nutrients (Chapin et al. 1990). Perennial grasses with clonal growth store carbohydrates in rhizomatous tissues as well as roots, and may mobilize these stores for future growth (White 1973; Klimes et al. 1993; Dong and de Kroon 1994). Studies of experimental defoliation in perennial grasses found regrowth yield and rate to be positively related to the amount of nitrogen (N) reserves (mainly amino acids and proteins; Millard 1988) available for mobilization (Ourry et al. 1994; Louahlia et al. 1999). High N storage in grasses may be an adaptation to environmental conditions of low or fluctuating avail-

ability of N (Thornton et al. 1993, 1994), and internal N conservation and recycling may lead to a degree of independence from soil nutrient supply (Tripathi and Singh 1994). Both carbon (i.e., biomass) and nutrient concentrations aid in assessment of reserves in plants; biomass allocation may not reflect nutrient allocation patterns (Abrahamson and Caswell 1982).

In salt marshes, a substantial portion of *Spartina* (cordgrass) biomass is found belowground, with root:shoot ratios generally >1 (Good et al. 1982) and as high as 49 in a short *S. alterniflora* marsh in Georgia (Gallagher 1974). Maximum belowground biomass typically occurs in winter with retranslocation of carbon and nitrogen compounds from senescing aboveground tissues to roots and rhizomes (Valiela et al. 1976; Schubauer and Hopkinson 1984; Anderson et al. 1997). Up to 35% of the belowground dry weight of *S. alterniflora* is composed of non-structural carbohydrates in winter (Livingstone and Patriquin 1981); the stored energy helps to produce a new canopy in spring (Hull et al. 1976; Lytle and Hull 1980; Hopkinson and Schubauer 1984). Gallagher and Howarth (1987) measured *S. alterniflora* underground reserves as regrowth when plants were placed in the

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dark; an estimated 23% of peak aerial biomass was recovered from storage products.

Studies of *Spartina* responses to fertilizer additions commonly conclude that growth is N-limited (Gallagher 1975; Valiela et al. 1985; DeLaune and Pezeshki 1988; Osgood and Zieman 1993; Dai and Wiegert 1996; Boyer and Zedler 1998). In *S. alterniflora*, mobilization from belowground tissues supplies a significant portion (54%) of the N needed for aerial growth (Hopkinson and Schubauer 1984), and combined with remineralization of macroorganic matter, can supply 75% of the plant's annual N demand (White and Howes 1994). Soil organic matter is highly correlated with soil total N (Cantilli 1989), and decomposing root and rhizome material represents a large, potentially-available N pool.

At salt marsh restoration sites, biomass accumulation and N recycling from both live and dead belowground tissues could be important to the successful establishment of new plants. Wetlands constructed for *Spartina* species may have sandy soils that are low in organic matter and N (Lindau and Hossner 1981; Craft et al. 1988; Langis et al. 1991); conservation and recycling of N from belowground tissues might be especially important at such sites. While *Spartina* spp. are common targets for restoration, only a few studies (of *S. alterniflora*) have estimated belowground biomass at created marshes (Broome et al. 1986; Craft et al. 1999; LaSalle et al. 1991; Seliskar unpublished data), and we know of none that has examined tissue N storage.

There are limited data on *Spartina foliosa* (Pacific cordgrass) belowground biomass (Mahall and Park 1976; Callaway and Josselyn 1992); nothing is known of either belowground tissue mass or N content in southern California marshes. In southern California, *S. foliosa* planted to constructed marshes is short compared to adjacent natural marshes (Zedler 1993). Canopies grow tall with N fertilization during the growing season but resume their short stature the next year if fertilization ceases (Boyer and Zedler 1998). The sandy soils in these constructed marshes have low organic matter content (Cantilli 1989; Langis et al. 1991) and low soil N (Boyer and Zedler 1998; Zedler and Callaway 1999) compared to natural marshes.

We hypothesized that live and dead belowground tissues in constructed marshes would increase with time, improving the storage and recycling of reserves, increasing the pool of remineralizable organic matter, and eventually sustaining robust aerial growth. Accumulation of fine sediments (with high N retention capacity) over time should also increase N supply to plants. Further, we hypothesized that additions of N fertilizer

would increase belowground storage of N and/or biomass accumulation in the constructed marshes.

To test the hypothesis that belowground stores would accumulate with time, we measured *S. foliosa* belowground biomass (live + dead) and N concentration in a natural marsh and in two constructed salt marshes (planted in 1985 and 1990) during winter 1995. Sediment texture with depth was examined to determine if fine sediments are accumulating with time. We took advantage of a large-scale fertilization project started in 1995 in the older constructed marsh to help evaluate whether N additions over 2 yr boost stores of belowground biomass or N.

Methods

STUDY LOCATION

This study was conducted in constructed and natural intertidal salt marshes of Sweetwater Marsh National Wildlife Refuge on San Diego Bay, California (Fig. 1). Connector Marsh (4.9 ha) was excavated from dredged material in 1984 (planted in spring of 1985) and Marisma de Nación (6.9 ha) was constructed similarly in 1990. Both wetlands were created to mitigate damages caused by highway and flood control channel construction. Our study was undertaken partly to compare these constructed marshes to the adjacent natural marsh, Paradise Creek (10 ha).

Sediments in the constructed marshes are coarse, ranging from loam to sandy loam (Swift 1988), with about 2.5% organic matter in 1990 (Pacific Estuarine Research Laboratory [PERL] unpublished data). Natural marsh sediments were characterized as clay loam in 1987 (Swift 1988) and had about 6.5% organic matter in 1990 (Langis et al. 1991; PERL unpublished data).

BELOWGROUND TISSUES

In mid-January 1995, 4 stands of *S. foliosa* were cored in each of the 3 marshes. Areas of pure *S. foliosa* were selected for study. Elevations were not determined as this species occurs as a monoculture only at lower elevations. Within each stand, 3 soil cores (15-cm diam, 40-cm deep) were collected using a razor-edged aluminum corer (Hargis and Twilley 1994). In Paradise Creek Marsh, the 4 stands sampled corresponded with 4 transects that have been used for long-term monitoring of *S. foliosa* height (PERL unpublished data). The 3 cores were collected from random positions along a line 1 m away from each long-term monitoring transect. In both created marshes, 3 positions were randomly selected for coring within each of the 4 cordgrass stands in each marsh.

Cores were sectioned every 10 cm in the field, bagged and returned to the lab, then rinsed over

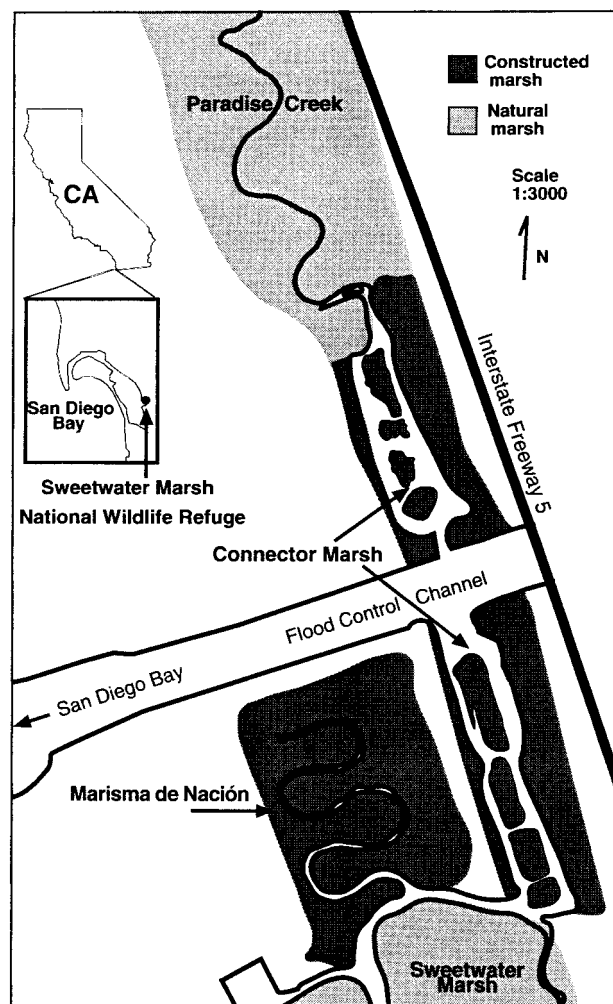


Fig. 1. Sweetwater Marsh National Wildlife Refuge, located on San Diego Bay between 24th Street in National City and E Street in Chula Vista, California (32°40'N, 117°5'W).

a 1-mm sieve to remove soil from belowground tissues. Live + dead belowground tissues were dried at 60°C to a constant mass, then weighed. We pooled live and dead tissue as we were interested in total accumulation as an indicator of marsh restoration progress relative to a natural wetland site; plants may tap live reserves or use nutrients remineralized from organic matter to support aerial growth.

For 2 of the 4 stands cored in each marsh (randomly-selected), N concentrations of the tissues were determined. Subsamples from each 10-cm section of tissue were ground with a Wiley mill through a 40-mesh sieve and then analyzed for total Kjeldahl nitrogen (TKN) (QuickChem Method 13-107-06-2-D) using a Lachat autoanalyzer (Model #2100-000). N crop was calculated as the %N (as a proportion) \times mass of each section.

In mid-January 1996 and 1997, we repeated the coring in Paradise Creek Marsh at sites 1 and 3. Paradise Creek Marsh was sampled to 40 cm again and evaluated as in 1995. Marisma de Nación was not sampled after 1995.

At Connector Marsh, we took advantage of a large-scale fertilization project to help evaluate the effects of N additions on belowground tissue stores. In spring of 1995, managers of the refuge identified stands of *S. foliosa* deemed large enough ($>400 \text{ m}^2$) to support home ranges of the light-footed clapper rail (*Rallus longirostris levipes*) (Boyer et al. 1996; Phinn et al. 1996; Boyer and Zedler 1998). At these stands, urea fertilizer ($\text{CO}(\text{NH}_2)_2$; 46% N by mass; 15 g N m^{-2}) was broadcast bi-weekly from March to August (1995 and 1996) with an Earthway spreader from atop a series of boardwalks. Two of these *S. foliosa* patches had been cored for the present study earlier in the year. As a portion of these 2 stands still remained unfertilized, we continued to sample them in January 1996 and 1997 (3 cores each, randomly selected locations) to compare to our 1995 data. We also cored the fertilized areas to examine responses in belowground tissue after 1 and 2 growing seasons of N additions.

In 1996 and 1997, Connector Marsh cores were taken only to 30-cm depth, as $<1\%$ of the mass in 1995 occurred deeper. All other sample processing was as before. We calculated the amount of the added N incorporated into belowground tissues by subtracting the mean N crop of the unfertilized areas from that of the fertilized areas and dividing by 300 (the total g of N added over 2 yr).

Root:shoot ratios were estimated based on total (live + dead) root and rhizome mass in winter (current study, January 1995) and peak aerial biomass in late summer (PERL unpublished data from August 1994). Aerial biomass was estimated from stem length measures using a stem length to biomass regression ($\log [\text{biomass}] = 1.683 \times \log [\text{stem length}] - 2.743$; $n = 60$; adjusted $r^2 = 0.95$).

SEDIMENT NITROGEN

Associated with the N addition experiment in Connector Marsh, sediment N concentration was determined after fertilizing for 1 growing season (1995, sampled August 18, 1995) and 2 growing seasons (1995 and 1996, sampled August 14, 1996). Within each fertilized or unfertilized cordgrass stand, 10 cores (5-cm diam) were taken to a depth of 10 cm, dried at 80°C, ground, and analyzed for TKN as above.

SEDIMENT TEXTURE

A 10-cm diam corer was used to collect samples for sediment texture analysis in mid-March and

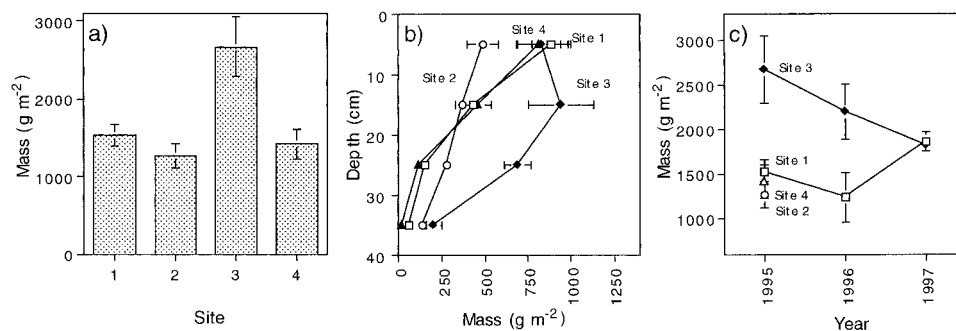


Fig. 2. *Spartina foliosa* belowground tissue mass at Paradise Creek Marsh as mean total mass in 1995 (a), distribution of mass by depth (b), and total mass sampled over three years (c). Values are means of three cores per site \pm SE.

mid-August 1995. At 4 cordgrass stands within each marsh (Paradise Creek Marsh, Connector Marsh, and Marisma de Nación), 4 cores were collected to 10-cm depth, and an additional core was taken to 30 cm. All cores were sectioned in 2-cm increments in the field. Samples were returned to the lab and dried at 80°C. Particle size analysis was performed by the hydrometer method (Bouyoucos 1962; Gee and Bauder 1986).

STATISTICAL ANALYSES

Belowground tissue N concentration, biomass, and N crop were examined using ANOVA (SuperANOVA version 1.11 for Macintosh). Data from Paradise Creek Marsh, Connector Marsh, and Marisma de Nación were compared in 1995 using 2-factor ANOVA, with marsh and depth as factors, on means for the 3 cores per cordgrass stand. Four stands were sampled for biomass in all marshes in 1995; 2 each were sampled for tissue nutrients and N crop. The 2 stands in Paradise Creek Marsh that were sampled again in 1996 and 1997 were compared to the two unfertilized Connector Marsh stands in those years (2-factor ANOVA; marsh, depth). The fertilized and unfertilized areas were compared graphically; this management project was not designed as an experiment for which statistical analyses were appropriate. Percent clay content of soils in the top 10 cm (1995 only) was com-

pared by 2-factor ANOVA (marsh, depth). Tests were considered significant if $p < 0.05$. Interactions were not significant unless noted. Residuals were examined and data were transformed to improve homoscedasticity (log transformation on N concentration, biomass, and sediment texture; log $[x + 1]$ on belowground N crop data). Tukey's honestly significantly different test was used to make multiple comparisons after a significant ANOVA.

Results

BELOWGROUND TISSUES

Natural Marsh

In 1995, belowground biomass (to a depth of 40 cm) within the natural Paradise Creek Marsh ranged from 1269 ± 154 to 2668 ± 377 g m⁻² (mean \pm SE) at the 4 sites, with an overall mean of 1719 ± 239 g m⁻² (Fig. 2a). Variability was high among sites, both in total mass (Fig. 2a) and in distribution with depth (Fig. 2b). Interannual variability within a site was also high, but mean total mass for Paradise Creek Marsh was similar among years (Fig. 2c).

Using the stem length to biomass regression described in the methods section, aerial mass in August 1994 was 620 ± 195 g m⁻². Coupled with the mean belowground mass in the following winter (January 1995), the root:shoot ratio was 2.8 (1719:620) at Paradise Creek Marsh (Table 1).

N concentrations in the tissues were similar among Paradise Creek Marsh sites 1 and 3 (10.8 ± 0.7 and 11.0 ± 0.8 mg N g dry tissue⁻¹, respectively), the 2 sites that were analyzed for N content. N crop (% N \times mass) differed at the 2 sites (16.6 ± 0.6 and 29.1 ± 4.1 g N m⁻², respectively), largely due to differences in biomass (Fig. 2a).

Constructed Marshes

In 1995, belowground biomass at both of the constructed marshes was lower than at Paradise

TABLE 1. *Spartina foliosa* root mass, shoot mass, and root:shoot ratios for the natural marsh, Paradise Creek (PC), the 10-year old Connector Marsh (CM), and the 5-year old Marisma de Nación (MN) in 1995. Root mass is the mean total (live + dead) belowground mass (g). Shoot mass is the mean peak aerial mass (August 1994) estimated from a stem length-to-biomass regression (see methods) (g). Standard error is in parentheses.

	Root Mass	Shoot Mass	Root:Shoot Ratio
PC	1719 (239)	620 (195)	2.8
CM	1532 (219)	90 (35)	17.0
MN	1005 (150)	485 (14)	2.1

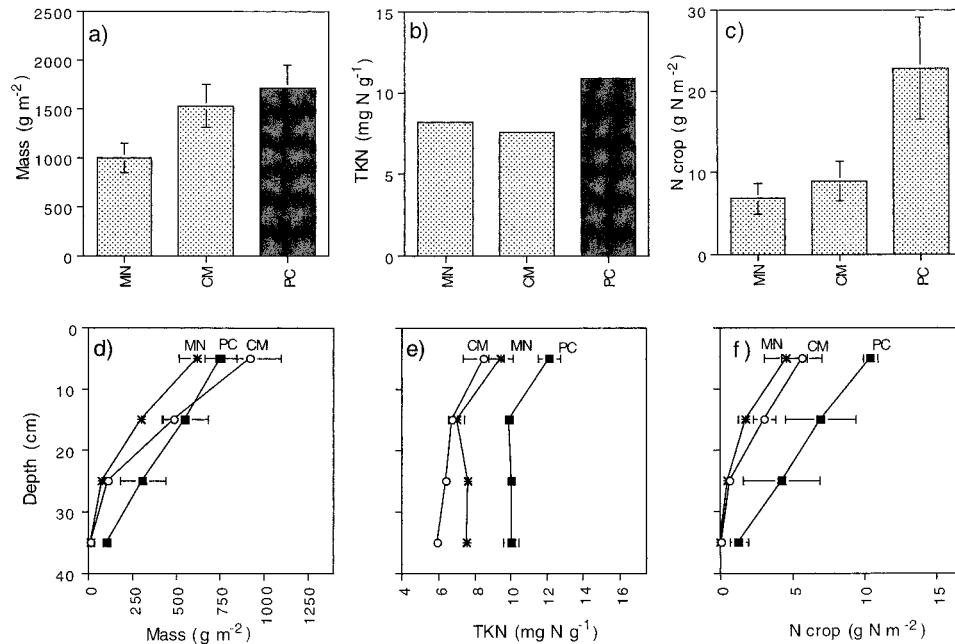


Fig. 3. Total mass (a), total Kjeldahl nitrogen (TKN) (b), and nitrogen crop (c) of *Spartina foliosa* root and rhizome tissues at Marisma de Nación (MN), Connector Marsh (CM), and Paradise Creek (PC) Marsh in January 1995. The two constructed marshes are indicated by lighter bars. Panels d, e, and f show distributions by depth. Error bars are too small to appear in (b). For mass, values are means (four *S. foliosa* stands per marsh) of means (three cores each stand) \pm SE. N concentration was measured (and N crop calculated) for two of the stands in each marsh.

Creek Marsh ($p = 0.0008$; Tukey test, $p < 0.05$). The 5-year old constructed marsh, Marisma de Nación ($1,005 \pm 150 \text{ g m}^{-2}$), had 40% less biomass than the natural marsh ($1,719 \pm 239 \text{ g m}^{-2}$; Fig. 3a). Connector Marsh, 10 years after planting, was intermediate in total mass ($1,532 \pm 219 \text{ g m}^{-2}$; Fig. 3a). This pattern was generally consistent throughout the depths sampled, but Connector Marsh ranked higher than Paradise Creek Marsh in the top 10 cm (Fig. 3d). Roots in the natural marsh reached at least 10 cm deeper than in the constructed marshes (Fig. 3d).

Using our biomass regression equation on August 1994 stem length data, Connector Marsh aerial mass ($90 \pm 35 \text{ g m}^{-2}$) was about 6 \times lower than at Paradise Creek Marsh ($620 \pm 195 \text{ g m}^{-2}$) (Table 1). The root:shoot ratio for Connector Marsh was 17 (1532:90). This ratio is about 6 \times that calculated for Paradise Creek (ratio of 2.8). At Marisma de Nación, aboveground mass was estimated to be $495 \pm 14 \text{ g m}^{-2}$. The root:shoot ratio was 2.1 (1005:485), more similar to that of Paradise Creek Marsh than Connector Marsh (Table 1).

Both constructed marshes had lower tissue N concentration (approximately 8 mg N g^{-1}) than Paradise Creek Marsh ($10.9 \pm 0.1 \text{ mg N g}^{-1}$; $p = 0.0001$; Tukey test, $p < 0.05$, Fig. 3b). Tissue N was about 40% lower in the constructed marshes throughout the 40-cm depth cores (Fig. 3e). Mar-

isma de Nación exceeded Connector Marsh in N concentration at most depths. Tissue N was higher at the surface (0–10 cm) than deeper ($p = 0.0001$; Tukey test, $p < 0.05$).

Both constructed marshes were significantly lower in mean total N crop belowground (approximately 7–9 g N m^{-2}) than Paradise Creek Marsh (Fig. 3c; $p = 0.0005$; Tukey test, $p < 0.05$). Paradise Creek Marsh was greater in N crop through all depths (Fig. 3f). For all marshes, N crop decreased significantly with each 10-cm depth increment (Tukey test, $p < 0.05$).

In 1996 and 1997, when only Paradise Creek Marsh and Connector Marsh unfertilized areas were compared statistically, the constructed marsh continued to have lower belowground biomass than the natural marsh when examined by depth ($p = 0.0028$ in 1996 and 0.0001 in 1997; Figs. 4a,d and 5a,d). Tissue N concentration remained lower in Connector Marsh in both 1996 ($p = 0.0002$; Fig. 4b,e) and 1997 ($p = 0.0028$; Fig. 5b,e). N crop was also lower in Connector Marsh both years ($p = 0.03$ in 1996 and 0.0077 in 1997; Figs. 4c,f and 5c,f). In general, biomass, tissue N concentration, and N crop were greatest near the soil surface, declining gradually with depth (Figs. 4d-f and 5d-f).

Fertilized and Unfertilized Areas

Fertilization of the constructed Connector Marsh during the 1995 growing season did not ap-

pear to increase belowground biomass, as measured in January 1996 (Fig. 4a). Tissue N concentrations suggested an approximately 10% increase with fertilization (Fig. 4b), largely at the 0–10 and 10–20 cm depths (Fig. 4e). There was a trend of increased N crop with N additions (Fig. 4c), especially in the top 10 cm (Fig. 4f), but variability was high.

In January 1997, after 2 years of applying fertilizer during the growing season, belowground biomass continued to be similar in the fertilized and unfertilized plots (Fig. 5a,d). N concentration remained elevated with N additions (Fig. 5b), but N crop continued to be similar with or without fertilization throughout the top 30 cm (Fig. 5c,f). While N additions over 2 growing seasons appeared to increase belowground tissue N concentration in Connector Marsh, N crop remained about half that of the natural marsh (Fig. 6).

Of the 300 g N m⁻² yr⁻¹ added to Connector Marsh over 2 growing seasons, only 3 g N m⁻² (< 2%) were trapped in belowground biomass in winter. N concentrations in the soil did not increase with fertilization (Table 2), although levels were higher in 1996 than 1995.

FINE-SEDIMENT ACCRETION

The accumulation of N belowground might be improved by the accretion of fine sediments at the soil surface, because the clay component of the soil has the greatest cation exchange capacity and potential for nutrient retention. The clay component in the soil was significantly greater in Paradise Creek Marsh than in either of the constructed marshes (Fig. 7; $p = 0.0001$). At Paradise Creek Marsh, soils were about 40–45% clay, with higher variability in clay content at depth. Silt made up 25–30%, and sand was generally 30%.

Soils at the constructed wetlands were coarse, although fine soils were found on the surface of the marsh. At depth (10–30 cm), soils at the Connector Marsh were approximately 15% clay, 35% silt, and 50% sand. Surface soils (0–2 cm depth) had about 40% clay, indicating the accumulation of mineral matter similar in texture to sediments at Paradise Creek Marsh. The clay component of the soil dropped to 27% in the 2–4 cm section of the soil, and then to 13–20% clay in deeper sections. In the 11 years since Connector Marsh was excavated, approximately 4 cm of material had accumulated.

At Marisma de Nación, sediments in the 0–2 cm soil sections were high in clay (40%), with 32% at 2–4 cm and 22% at 4–6 cm. The clay component of the soil dropped sharply below 6 cm (to 10–15% clay), suggesting that up to 6 cm of material may

have deposited on the marsh surface in the 5 years following construction.

Discussion

COMPARISONS OF NATURAL *SPARTINA* MARSHES

At Paradise Creek Marsh, *S. foliosa* belowground biomass values were considerably lower than in most studies of *Spartina* marshes of the eastern U.S. in fall/winter (Table 3). However, our values for southern California were up to twice those for *S. foliosa* in San Francisco Bay (Mahall and Park 1976; Callaway and Josselyn 1992) (Table 3).

Variability was high in this study and might be attributed to a variety of factors, e.g., interannual changes in mean sea level or rainfall (Morris and Haskin 1990), intra-marsh differences in soil conditions or history of sediment deposition (Gallagher and Plumley 1979), and the clumped growth pattern of *Spartina*. Two-fold differences in biomass were found beneath versus between clumps for *S. cynosuroides* (Gallagher and Plumley 1979) and *S. alterniflora* (Roman and Daiber 1984).

The Paradise Creek Marsh root:shoot ratio of 2.8 (1719:620) is at the low end of the range found for *S. alterniflora*, *S. cynosuroides*, and *S. patens*. Most ratios are approximately 4–11 (see review in Good et al. 1982; Schubauer and Hopkinson 1984; Anderson et al. 1997) and reach as high as 49 (short *S. alterniflora*; Gallagher 1974). Callaway and Josselyn (1992) found a ratio of 5.1 (1386:271) for one northern California *S. foliosa* marsh (San Francisco Bay) and 1.9 (549:290) for another. Our root:shoot ratio fell between the two northern California marshes, but our belowground mass values tended to be higher (approximately 1,300–2,700 g m⁻²).

N concentrations found in this study were similar to those reported by Roman and Daiber (1984) for live + dead belowground *S. alterniflora* (tall form: 10.4 ± 0.4 mg N g⁻¹; short form: 9.5 ± 0.4 mg N g⁻¹) and *S. patens* (11.4 ± 0.4 and 10.6 ± 0.3 mg N g⁻¹ at two marshes). Studies of live *S. alterniflora* belowground tissues report lower N concentrations; e.g., 6 mg N g⁻¹ in live roots + rhizomes (White and Howes 1994) and 6.9 mg N g⁻¹ in roots and 5.2 mg N g⁻¹ in rhizomes (Anderson et al. 1997). Hopkinson and Schubauer (1984) also report N concentrations of approximately 5.0 mg N g⁻¹ and note that similar N concentrations were found in both live and dead belowground tissues.

COMPARISONS OF CONSTRUCTED *SPARTINA* MARSHES

At the constructed marshes, we found *S. foliosa* belowground biomass to be lower than in constructed *S. alterniflora* marshes (Table 3). Except for one case where values were similar to this study (Seliskar unpublished data, short form at 3 years),

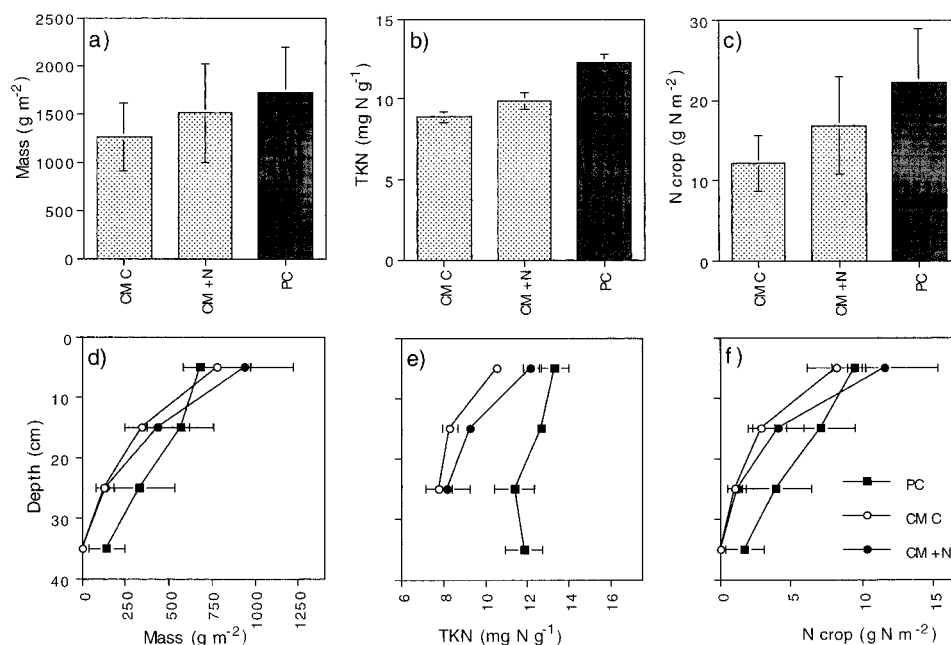


Fig. 4. Total mass (a), total Kjeldahl nitrogen (TKN) (b), and nitrogen crop (c) of *Spartina foliosa* root and rhizome tissues at Connector Marsh control areas (unfertilized) (CM C), Connector Marsh N-fertilized areas (CM +N), and Paradise Creek (PC) Marsh in January 1996. The constructed marsh is indicated by lighter bars. Figures d, e, and f show distributions by depth. CM +N areas were fertilized during the growing season in 1995. Values are means (two *S. foliosa* stands) of means (three cores per stand) \pm SE.

our values were about half as high, even though the *S. alterniflora* marshes were often younger than ours. In general, *S. foliosa* appears to have lower belowground accumulation than other *Spartina*

species, whether the marshes are natural or constructed. We know of no other *S. foliosa* belowground data for constructed marshes to use in comparison.

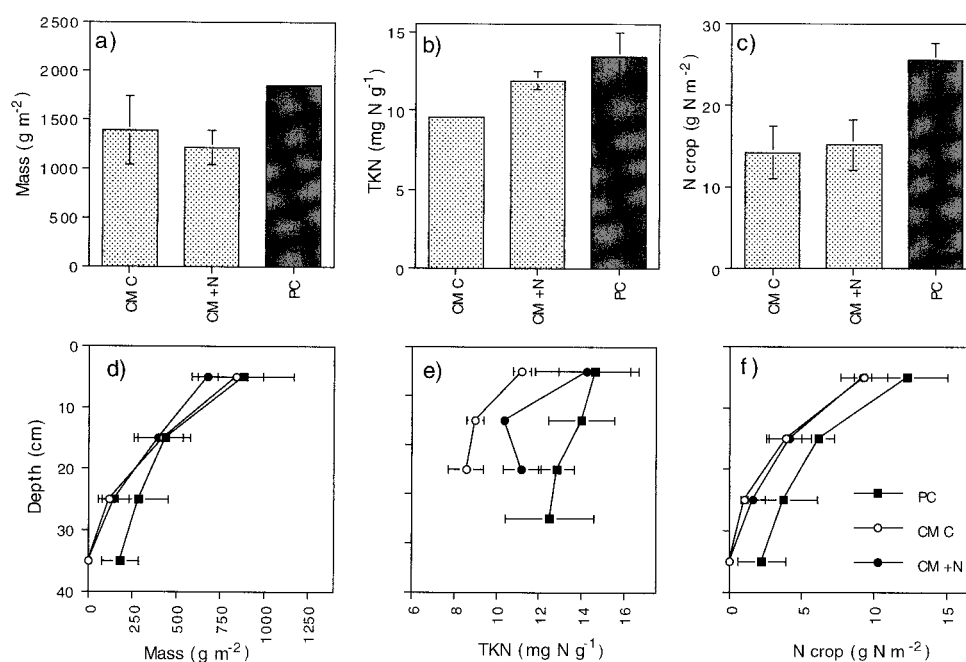


Fig. 5. Same as Fig. 4 but for January 1997. CM +N areas were fertilized during both the 1995 and 1996 growing seasons.

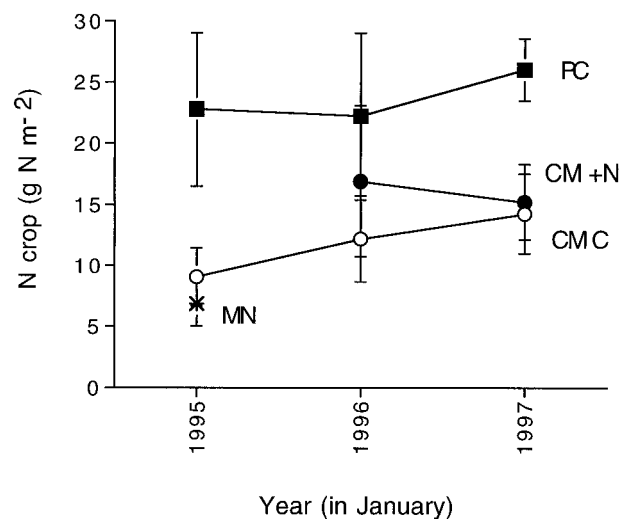


Fig. 6. Mean total belowground nitrogen crop (\pm SE) over three years. Marisma de Nación (MN) was sampled only in 1995. Connector Marsh control areas (unfertilized) (CM C) and Paradise Creek (PC) Marsh were sampled in all years. Connector Marsh N-fertilized areas (CM +N) were sampled in 1996 after fertilization for one growing season, and in 1997 after two.

Compared to the *S. alterniflora* constructed marshes described in the literature, Connector Marsh's *S. foliosa* root:shoot ratio is high, but Marisma de Nación's is similar. LaSalle et al. (1991) found root:shoot ratios of 2.5 (2204:856) for a 4-yr old *S. alterniflora* marsh and 4.8 (3061:631) for an 8-yr old marsh. Broome et al. (1986) found the ratio to be <1 for the first 2 yr of establishment, increasing to an average of 2.7 in the latter 5 yr sampled in a 10-yr old marsh. This ratio was very similar to that of their natural marsh comparison site (2.5).

PROGRESS OF *S. FOLIOSA* CONSTRUCTED MARSHES

Over the 3-yr study, Connector Marsh cordgrass had, on average, 79% of the belowground biomass of Paradise Creek Marsh; however, belowground N crop was only 53% of Paradise Creek levels (Fig. 6). Still, belowground development is more similar in the two marshes than is peak aerial mass (approximately $6\times$ lower in Connector Marsh; Table 1). It is not clear why Connector Marsh had such low shoot mass. Marisma de Nación produced a more robust canopy of *S. foliosa* than Connector Marsh in 1995 (Table 1), even though it is a younger constructed marsh with lower belowground biomass (Fig. 3a).

We suggest that the confined nature of the two constructed marshes helps to explain these findings. Originally, the constructed marshes were excavated to elevations appropriate for cordgrass growth. As sediment accreted, elevation became

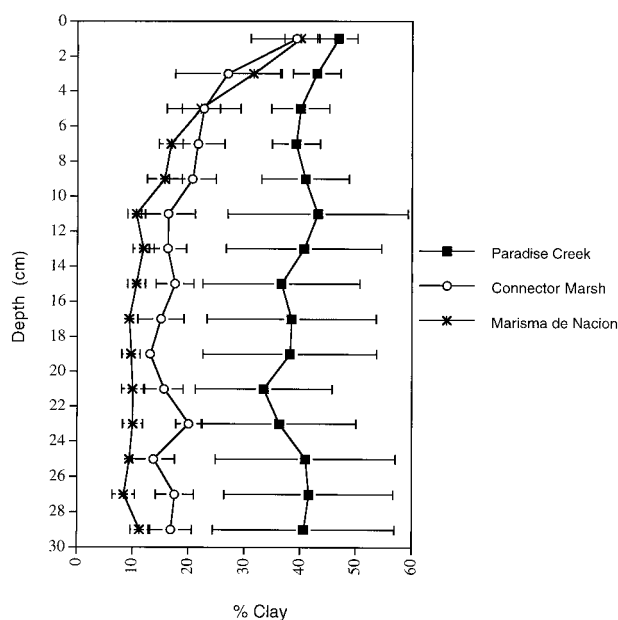


Fig. 7. Percent of clay soil particles with depth at the three marshes in 1995. Values are means (four *Spartina foliosa* stands) of means (five cores per stand) to 10-cm depth. Values for 10–30 cm depths are means (four *S. foliosa* stands) of one core per stand. Bars are (\pm SE).

unfavorable for *S. foliosa*; this is evidenced by a decreasing area of cordgrass at Connector Marsh and expansion of competing succulents (Haltiner et al. 1997; Boyer and Zedler 1999). Marisma de Nación also appears to be decreasing in cordgrass area (Boyer personal observation); aerial mass dropped from 485 g m^{-2} in 1995 to 220 g m^{-2} in 1996 (PERL unpublished data), perhaps indicating a declining trend. Neither marsh has mudflats that might allow *S. foliosa* to spread downslope. In contrast, historical photos show that Paradise Creek Marsh has its most robust cordgrass in an area that has very gradually accreted to its current elevation.

It is important to note that there are other differences between the sites that could restrain convergence of biotic and abiotic characteristics at the constructed and natural sites. For example, there are greater velocity flows (Haltiner et al. 1997) and higher densities of at least one *S. foliosa* herbivore (Boyer and Zedler 1996) at Connector Marsh than

TABLE 2. Soil TKN (total Kjeldahl nitrogen) in Connector Marsh after N additions during one or two growing seasons (1995 only or 1995 + 1996), or with no N added. Values are means (two *Spartina foliosa* stands) of means (ten 10-cm deep cores each) with (SE). Units are mg N g^{-1} dry soil.

Sampling Date	No N Added	N Added
Aug 1995	0.79 (0.01)	1.10 (0.30)
Aug 1996	1.02 (0.12)	1.26 (0.37)

TABLE 3. Mean values of total (live + dead) belowground biomass in *Spartina* species in fall or winter.

Species and Study	Location	Month	Mean Mass (g m ⁻²)	Notes
Natural marshes				
<i>S. alterniflora</i>				
Anderson et al. 1997	Virginia	Dec	5,455	
Capehart and Hackney 1989	North Carolina	(not given)	5,100	
Craft et al. 1999	North Carolina	Oct	~2,100/~3,900	two marshes
Gallagher 1974	Georgia	(not given)	2,243/14,594/14,655	tall/medium/short form (one marsh)
Gross et al. 1991	Delaware	Nov	4,600/6,500	tall/short form (one marsh)
Roman and Daiber 1984 ^a	Delaware	(variable)	12,400/9,400	tall form (two marshes)
			19,300/14,300	short form (two marshes)
Schubauer and Hopkinson 1984	Georgia	Dec	~6,200	
<i>S. cynosuroides</i>				
Capehart and Hackney 1989	North Carolina	(not given)	6,300	
Gallagher and Plumley 1979	Georgia	Dec–Feb	3,800–6,500	cores taken between stems
			7,500–12,000	cores taken over stems
Hackney and de la Cruz 1986	North Carolina	Feb/Nov	7,000/7,250	(same marsh, two different months)
Schubauer and Hopkinson 1984	Georgia	Feb	~8,300	
<i>S. foliosa</i>				
Boyer et al. (this study) ^c	Southern California	Jan	1,719/1,719/1,844	one marsh (1995–1996–1997)
Callaway and Josselyn 1992	Northern California	Nov	1,386/549	two marshes
Mahall and Park 1976 ^b	Northern California	Nov	1,024/1,300	two marshes
<i>S. patens</i>				
Roman and Daiber 1984 ^a	Delaware	(variable)	6,000/4,700	one marsh (1975–1976)
			20,800/12,100	one marsh (1975–1976)
Created marshes				
<i>S. alterniflora</i>				
Broome et al. 1986	North Carolina	Oct	2,311/2,795	one marsh at 5 yr/10 yr
Craft et al. 1999	North Carolina	Oct	~2,400/~3,600	21-yr old marsh/25-yr old marsh
LaSalle et al. 1991	South Carolina	Sept	2,204/3,601	4-yr old marsh/8-yr old marsh
Seliskar unpublished data	Delaware	Sept	2,051	tall form at 3 yr
			1,322/2,255	short form at 3 yr/5 yr
<i>S. foliosa</i>				
Boyer et al. (this study) ^c	Southern California	Jan	1,531/1,257/1,383	one marsh at 10 yr (1995)/11 yr/12 yr
			1,005	5-yr old marsh (1995)

^a Values are maxima, not means.^b Median value for range of dead mass reported (80–350 g m⁻²) has been added here.^c Mass from 4 sites in 1995, 2 sites in 1996–1997.

at Paradise Creek. There will always be some differences between restoration and reference sites.

IMPLICATIONS FOR MANAGEMENT

At Connector Marsh, less than 2% of the added N was trapped in belowground tissues and N crop remained about half that of the natural marsh even with fertilization over two growing seasons (Fig. 6). These findings might suggest that availability of the added N was low, perhaps due to poor conversion by N-transforming microorganisms; however, the strong canopy response to urea in our related work (Boyer and Zedler 1998) suggests that availability and uptake were not limiting. The fact that the belowground tissue mass is approximately 80% of natural marsh levels at Connector Marsh suggests that live + dead tissues are accumulating with time,

yet N storage is low, and aerial growth is poor. We believe that the supply of N from the soil over time is a stronger determinant of *S. foliosa* canopy development than is belowground tissue mass.

Fine-textured sediments at the surface of the created marshes should improve overall N retention, but present deposits are well above the zone of greatest root and rhizome biomass (approximately 15–20 cm). As the marsh elevation continues to increase, species composition is likely to continue to shift from *S. foliosa* to *Salicornia virginica* and other succulents (Zedler 1977; Haltiner et al. 1997). Given these considerations, it is unlikely that sediment accumulation will significantly improve N pools for *Spartina* habitat at Connector Marsh. Overexcavation has been proposed at multiple San Francisco Bay restoration sites, including

the Sonoma Baylands (Williams 1986; Williams and Florsheim 1994), however, this estuary has very high suspended sediment loads and greater long-term rates of sediment accretion. In southern California, where sediments accumulate mostly from flood events, accretion rates are unpredictable in timing and magnitude (Zedler 1983; Cahoon et al. 1996; PERL unpublished data). We suggest salvaging and importing fine, organic marsh sediments or adding organic amendments to establish proper substrate conditions. If these options are not possible, overexcavating to allow for the eventual accretion of silt and clay might be attempted.

Most southern California wetlands lack *S. foliosa*, and destructive sampling is not encouraged in the few places where it does occur, because it would disturb nesting by endangered light-footed clapper rails. Our specific comparison grew out of a mitigation project, wherein the reference site was damaged and the 2 constructed sites were required to replace the qualities lost in part of the reference site. Environmental field studies are often constrained by number and/or size of comparable sites (Eberhardt and Thomas 1991); whenever possible, future studies should compare multiple restored and natural marshes (e.g., three or more of each type).

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LITERATURE CITED

- ABRAHAMSON, W. G. AND H. CASWELL. 1982. On the comparative allocation of biomass, energy and nutrients in plants. *Ecology* 63:982-991.
- ANDERSON, I. C., C. R. TOBIAS, B. B. NEIKIRK, AND R. L. WETZEL. 1997. Development of a process-based nitrogen mass balance model for a Virginia (USA) *Spartina alterniflora* salt marsh: Implications for net DIN flux. *Marine Ecology Progress Series* 159: 13-27.
- BOUYOUCOS, G. J. 1962. Hydrometer method improved for making particle size analyses of soils. *Agronomy Journal* 54:464-465.
- BOYER, K. E. AND J. B. ZEDLER. 1996. Damage to cordgrass by scale insects in a constructed salt marsh: Effects of nitrogen additions. *Estuaries* 19:1-12.
- BOYER, K. E. AND J. B. ZEDLER. 1998. Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecological Applications* 8:692-705.
- BOYER, K. E. AND J. B. ZEDLER. 1999. Nitrogen addition could shift plant community composition in a restored California salt marsh. *Restoration Ecology* 7:74-85.
- BOYER, K. E., J. B. ZEDLER, S. PHINN, G. D. WILLIAMS, G. B. NOE, S. TRNKA, AND B. FINK. 1996. The Status of Constructed Wetlands at Sweetwater Marsh National Wildlife Refuge. Annual Report to the California Department of Transportation and the U.S. Fish and Wildlife Service, Pacific Estuarine Research Laboratory, San Diego, California.
- BROOME, S. W., E. D. SENECA, AND W. W. WOODHOUSE. 1986. Long-term growth and development of transplants of the salt-marsh grass *Spartina alterniflora*. *Estuaries* 9:63-74.
- CAHOON, D. R., J. C. LYNCH, AND A. N. POWELL. 1996. Marsh vertical accretion in a southern California estuary, U.S.A. *Estuarine, Coastal and Shelf Science* 43:19-32.
- CALLAWAY, J. C. AND M. N. JOSSELYN. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in south San Francisco Bay. *Estuaries* 15:218-226.
- CANTILLI, J. F. 1989. Sulfide phytotoxicity in tidal salt marshes. Thesis, San Diego State University, San Diego, California.
- CAPEHART, A. A. AND C. T. HACKNEY. 1989. The potential role of roots and rhizomes in structuring salt-marsh benthic communities. *Estuaries* 12:119-122.
- CHAPIN III, F. S., E. D. SCHULZE, AND H. A. MOONEY. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21:423-447.
- CRAFT, C. B., S. W. BROOME, AND E. D. SENECA. 1988. Nitrogen, phosphorus and organic carbon pools in natural and transplanted marsh soils. *Estuaries* 11:272-280.
- CRAFT, C. B., J. READER, J. N. SACCO, AND S. W. BROOME. 1999. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications* 9: 1405-1419.
- DAI, T. AND R. G. WIEGERT. 1996. Ramet population dynamics and net aerial productivity of *Spartina alterniflora*. *Ecology* 77: 276-288.
- DELAUNE, R. D. AND S. R. PEZESHKI. 1988. Relationship of mineral nutrients to growth of *Spartina alterniflora* in Louisiana salt marshes. *Northeast Gulf Science* 10:55-60.
- DONG, M. AND H. DE KROON. 1994. Plasticity in morphology and biomass allocation in *Cynodon dactylon*, a grass species forming stolons and rhizomes. *Oikos* 70:99-106.
- EBERHARDT, L. L. AND J. M. THOMAS. 1991. Designing environmental field studies. *Ecological Monographs* 61:53-73.
- GALLAGHER, J. L. 1974. Sampling macro-organic matter profiles in salt marsh plant root zones. *Soil Science Society of America Proceedings* 38:154-155.
- GALLAGHER, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *American Journal of Botany* 62:644-648.
- GALLAGHER, J. L. AND R. W. HOWARTH. 1987. Seasonal differences in *Spartina* recoverable underground reserves in the Great Sippewissett Marsh in Massachusetts. *Estuarine, Coastal and Shelf Science* 25:313-319.
- GALLAGHER, J. L. AND F. G. PLUMLEY. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *American Journal of Botany* 66:156-161.
- GEE, G. W. AND J. W. BAUDER. 1986. Particle-size analysis, p. 383-411. In A. Klute (ed.), *Methods of Soil Analysis: Part I: Physical and Mineralogical Methods*. American Society of Agronomy, Madison, Wisconsin.
- GOOD, R. E., N. F. GOOD, AND B. R. FRASCO. 1982. A review of primary production and decomposition dynamics of the belowground marsh component, p. 139-157. In V. S. Kennedy (ed.), *Estuarine Comparisons*. Academic Press, New York.
- GROSS, M. F., M. A. HARDISKY, P. L. WOLF, AND V. KLEMAS. 1991. Relationship between aboveground and belowground biomass of *Spartina alterniflora* (smooth cordgrass). *Estuaries* 14: 180-191.
- HACKNEY, C. T. AND A. A. DE LA CRUZ. 1986. Belowground productivity of roots and rhizomes in a giant cordgrass marsh. *Estuaries* 9:112-116.
- HALTNER, J., J. B. ZEDLER, K. E. BOYER, G. D. WILLIAMS, AND J. C. CALLAWAY. 1997. Influence of physical processes on the

- design, functioning and evolution of restored tidal wetlands in California (USA). *Wetlands Ecology and Management* 4:73–91.
- HARGIS, T. G. AND R. R. TWILLEY. 1994. Improved coring device for measuring soil bulk density in a Louisiana deltaic marsh. *Journal of Sedimentary Research Section A: Sedimentary Petrology and Processes* 64:681–683.
- HOPKINSON, C. S. AND J. P. SCHUBAUER. 1984. Static and dynamic aspects of nitrogen cycling in the salt marsh graminoid, *Spartina alterniflora* Loisel. *Ecology* 65:961–969.
- HULL, R. J., D. M. SULLIVAN, AND R. W. LYTLE. 1976. Photosynthetic distribution in natural stands of salt water cordgrass. *Agronomy Journal* 68:969–972.
- KLIMES, L., J. KLIMESOVA, AND J. OSBORNOVA. 1993. Regeneration capacity and carbohydrate reserves in a clonal plant *Rumex alpinus*: Effect of burial. *Vegetatio* 109:153–160.
- LANGIS, R., M. ZALEJKO, AND J. B. ZEDLER. 1991. Nitrogen assessments in a constructed and a natural salt marsh of San Diego Bay, California. *Ecological Applications* 1:40–51.
- LASALLE, M. W., M. C. LANDIN, AND J. G. SIMS. 1991. Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. *Wetlands* 11:191–208.
- LINDAU, C. W. AND L. R. HOSSNER. 1981. Substrate characterization of an experimental marsh and three natural marshes. *Soil Science Society of America Proceedings* 45:1171–1176.
- LIVINGSTONE, D. C. AND D. G. PATRIQUIN. 1981. Belowground growth of *Spartina alterniflora* Loisel: Habit, functional biomass and non-structural carbohydrates. *Estuarine, Coastal and Shelf Science* 12:579–588.
- LOUAHLIA, S., J. H. MACDUFF, A. OURRY, M. HUMPHREYS, AND J. BOUCAUD. 1999. Nitrogen reserve status affects the dynamics of nitrogen remobilization and mineral nitrogen uptake during recovery of contrasting cultivars of *Lolium perenne* from defoliation. *New Phytologist* 142:451–462.
- LYTLE, R. W. AND R. J. HULL. 1980. Annual carbohydrate variation in culms and rhizomes of smooth cordgrass (*Spartina alterniflora* Loisel). *Agronomy Journal* 72:933–942.
- MAHALL, B. E. AND R. B. PARK. 1976. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay: I. Biomass and production. *Journal of Ecology* 64:421–433.
- MILLARD, P. 1988. The accumulation and storage of nitrogen by herbaceous plants. *Plant, Cell and Environment* 11:1–8.
- MORRIS, J. T. AND B. HASKIN. 1990. A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. *Ecology* 71:2209–2217.
- OSGOOD, D. T. AND J. C. ZIEMAN. 1993. Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. *Estuaries* 16:815–826.
- OURRY, A., T. H. KIM, AND J. BOUCAUD. 1994. Nitrogen reserve mobilization during regrowth of *Medicago sativa* L.: Relationships between their availability and regrowth yield. *Plant Physiology* 105:831–837.
- PHINN, S. R., D. A. STOW, AND J. B. ZEDLER. 1996. Monitoring wetland habitat restoration in southern California using airborne multispectral video data. *Restoration Ecology* 4:412–422.
- ROMAN, C. T. AND F. C. DAIBER. 1984. Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes. *Bulletin of the Torrey Botanical Club* 111:34–41.
- SCHUBAUER, J. P. AND C. S. HOPKINSON. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography* 29:1052–1065.
- SWIFT, K. L. 1988. Salt marsh restoration: Assessing a southern California example. Thesis, Diego State University, San Diego, California.
- THORNTON, B., P. MILLARD, AND E. I. DUFF. 1994. Effects of nitrogen supply on the source of nitrogen used for regrowth of laminae after defoliation of four grass species. *New Phytologist* 128:615–620.
- THORNTON, B., P. MILLARD, E. I. DUFF, AND S. T. BUCKLAND. 1993. The relative contribution of remobilization and root uptake in supplying nitrogen after defoliation for regrowth of laminae in four grass species. *New Phytologist* 124:689–694.
- TRIPATHI, S. K. AND K. P. SINGH. 1994. Productivity and nutrient cycling in recently harvested and mature bamboo savannas in the dry tropics. *Journal of Applied Ecology* 31:109–124.
- VALIELA, I., J. M. TEAL, C. COGSWELL, J. HARTMAN, S. ALLEN, R. VAN ETTEN, AND D. GOEHRINGER. 1985. Some long-term consequences of sewage contamination in salt marsh ecosystems, p. 301–316. In P. J. Godfrey, E. R. Kaynor, S. Pelczarski, and J. Benforado (eds.), *Ecological Considerations in Wetland Treatment of Municipal Wastewater*. Van Nostrand Reinhold, New York.
- VALIELA, I., J. M. TEAL, AND N. Y. PERSSON. 1976. Productivity and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21:245–252.
- WHITE, L. M. 1973. Carbohydrate reserves of grasses: A review. *Journal of Range Management* 26:13–18.
- WHITE, D. S. AND B. L. HOWES. 1994. Long-term ¹⁵N-nitrogen retention in the vegetated sediments of a New England salt marsh. *Limnology and Oceanography* 39:1878–1892.
- WILLIAMS, P. B. 1986. Hydrology in coastal wetland restoration design, p. 329–336. In J. A. Kusler, M. L. Quammen, and G. Brooks (eds.), *Proceedings of the National Wetland Symposium: Mitigation of Impacts and Losses*, New Orleans, Louisiana, October 8–10, 1986. Association of State Wetland Managers, New York.
- WILLIAMS, P. B. AND J. L. FLORSHEIM. 1994. Designing the Sonoma Baylands project. *Coast and Ocean* 10:19–27.
- ZEDLER, J. B. 1977. Salt marsh community structure in the Tijuana Estuary, California. *Estuarine and Coastal Marine Science* 5:39–53.
- ZEDLER, J. B. 1983. Freshwater impacts in normally hypersaline marshes. *Estuaries* 6:346–355.
- ZEDLER, J. B. 1993. Canopy architecture of natural and planted cordgrass marshes: Selecting habitat evaluation criteria. *Ecological Applications* 3:123–138.
- ZEDLER, J. B. AND J. C. CALLAWAY. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology* 7:69–73.

SOURCES OF UNPUBLISHED MATERIALS

- PACIFIC ESTUARINE RESEARCH LABORATORY (PERL). San Diego State University, 6495 Alvarado Road, Suite 106, San Diego, California 92182–1870.
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