WETLANDS, Vol. 21, No. 3, September 2001, pp. 315–326

SALICORNIA VIRGINICA IN A SOUTHERN CALIFORNIA SALT MARSH: SEASONAL PATTERNS AND A NUTRIENT-ENRICHMENT EXPERIMENT

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Abstract: *Salicornia virginica* (common pickleweed) is the dominant vascular plant of many saline marshes of the US west coast, yet little is known about seasonal patterns or abiotic factors controlling it. In a southern California salt marsh, quarterly sampling revealed strong seasonal trends, with 2x greater *S. virginica* biomass in summer than in winter. Tissue nitrogen (N) and phosphorus (P) concentrations were highest in winter and lower in spring and summer, suggesting a dilution of nutrients as plants accumulated biomass during the growing season. Despite high sediment nutrient levels in this marsh, an experiment examining N and P effects still found strong *S. virginica* responses to N applied biweekly for >1 year. Increases in succulent tissue biomass after N addition were first seen in April 1998 (after fertilization for 11 months); two-fold increases in biomass and the number of branches resulted by the end of the experiment in August 1998. Addition of N increased N concentration in the woody tissues when sampled in August. The N:P ratio increased with N addition beginning in winter (7 months after fertilization began) and continuing through the remainder of the experiment. Effects of P addition were less marked, as adding P did not result in biomass responses; however, it did influence tissue nutrient levels. These amendments increased P concentrations in the woody tissue in August 1998. In contrast to N amendments, which did not affect root nutrient concentrations, P addition led to increases in P content of root tissues in the latter portion of the growing season. These data suggest that increases in nutrients (especially N, but also P) can lead to large changes in *S. virginica* characteristics even in estuaries with high sediment nutrient levels.

Key Words: California, nutrients, nitrogen, phosphorus, pickleweed, *Salicornia*, salt marsh, sediments, wetland

INTRODUCTION

In saline coastal marshes of the western United States, *Salicornia virginica* L. (common pickleweed) dominates the middle elevation marsh plain, is often the lowest-occurring emergent plant species, and is a common member of the high marsh plant community (Zedler 1982, Seliskar and Gallagher 1983, Onuf 1987). A perennial, C_3 succulent, *S. virginica* has a wide geographical range along the Pacific coast, from Puget Sound, Washington to the southern tip of Baja California, Mexico (Macdonald and Barbour 1974). *Salicornia virginica* provides important habitat for local birds throughout its range, including the black rail (*Laterallus jamaicensis* Gmelin), the California clapper rail (*Rallus longirostris obsoletus* Ridgway), and the light-footed clapper rail (*R. l. levipes*) (Small 1994), as well as a suite of migratory birds that forage within its canopy (Zedler et al. 1992). In southern California, it provides the primary habitat for the endangered Belding's Savannah sparrow, *Passerculus sandwichensis beldingi* Ridgway, which builds its nests beneath the plant canopy and perches on the taller plants (Powell 1993). *Salicornia virginica* is a major food source for marsh detritivores (Kwak and Zedler 1997, Page 1997). The plant canopy serves as a refuge from predation for invertebrates such as the lined shore crab, *Pachygrapsus crassipes* Randall (Willason 1981, Sousa 1993). As a dominant plant with many habitat values, *S. virginica* is a common focus of restoration projects in the region (e.g., Berger 1990, Zedler 1996).

Despite the importance of *S. virginica* in western marshes, there has been little experimental work on

the abiotic factors controlling it. In contrast, much is known about the chemical and physical factors controlling smooth cordgrass (*Spartina alterniflora* Loisel), the dominant plant of lower intertidal salt marshes on the US east and gulf coasts (Matthews and Minello 1994). One important factor is nutrient availability; many studies have found nitrogen (N) to limit *S. alterniflora* productivity or biomass (Sullivan and Daiber 1974, Valiela and Teal 1974, Broome et al. 1975, Gallagher 1975, Patrick and DeLaune 1976, Chalmers 1979, Haines 1979, Buresh et al. 1980, de la Cruz et al. 1981, Valiela et al. 1985, Dai and Wiegert 1996). Phosphorus (P) was added in a few of these studies (Sullivan and Daiber 1974, Valiela and Teal 1974, Broome et al. 1975, Patrick and DeLaune 1976, Buresh et al. 1980) but did not affect biomass accumulation except in sandy, constructed *Spartina alterniflora* marshes (North Carolina: Broome et al. 1975). Phosphorus limitation may have occurred after N addition relieved N limitation (Broome et al. 1975).

A number of studies of plant responses to nutrients on the west coast have focused on Pacific cordgrass, *Spartina foliosa* Trin. Compared to the body of evidence suggesting N limitation in *Spartina alterniflora*, studies of *S. foliosa* have produced mixed results. Nitrogen addition had no effect on *S. foliosa* biomass in a natural marsh near San Diego Bay but did increase the proportion of tall stems there (Boyer and Zedler 1998). At Tijuana Estuary, fertilization of two pure stands of *S. foliosa* produced large biomass increases in June, but only one stand continued to show an increase in August (Covin and Zedler 1988). *Spartina foliosa* planted to a marsh at Tijuana Estuary did not respond to N addition (Nordby et al. 1980). However, in sandy constructed marshes with low sediment nutrients on San Diego Bay, *S. foliosa* showed strong biomass responses to N addition (Gibson et al. 1994, Boyer and Zedler 1998, 1999). None of these studies examined P effects.

While *Salicornia virginica* is more abundant than *Spartina foliosa* in west coast marshes (both in areal extent and number of marshes where it occurs), the manner in which nutrients affect *S. virginica* is little known. Only one published study has examined nutrient effects directly; Covin and Zedler (1988) concluded that N limits *S. virginica* after biomass responses to fertilizer additions. Other correlative work suggests a positive relationship between N and *S. virginica* growth; in a study of natural abundances of ^{15}N, Page (1995) found that *S. virginica* tissues tracked gradients in watershed-derived N inputs. We are aware of no published data on P effects. Neither are there data on seasonal changes in soil or tissue nutrient distributions or nutrient demand.

Considering the many values of *S. virginica* marshes, the paucity of information on their characteristics and responses to abiotic conditions is surprising. As human-derived nutrient inputs increase in many coastal watersheds (National Academy of Sciences 1994), a better understanding of plant responses to nutrients is warranted. The objectives of this study were (1) to characterize a *Salicornia virginica* marsh north of Los Angeles, California, including seasonal patterns in biomass, stand structure, tissue nutrients, and sediment nutrients and (2) to test the effects of both N and P additions (alone and together) on *S. virginica* and sediment characteristics.

METHODS

This study took place in a pure stand of *Salicornia virginica* at Mugu Lagoon (34°06‘N, 119°05‘W) on the Naval Base Ventura County (NBVC), approximately mid-way between Santa Barbara and Santa Monica, California. A boardwalk system was installed to reduce trampling effects, and 20 experimental plots (1.5 x 1.5 m) were established, with the same size plot allowed as a buffer between them. Five of these plots were not manipulated (controls) and were examined for natural nutrient levels and seasonal patterns.

Each of the 20 plots was subjected to one of four treatments (5-fold replication): additions every two weeks of N, P, both N and P, or neither N nor P (controls). Nitrogen was applied as urea (46% N by mass; 15 g $N/m^2/2wk$). The application rate was similar to that of previous fertilization studies in southern California salt marshes (Covin and Zedler 1988, Boyer and Zedler 1998) and at the high end of the range used in studies on the east and gulf coasts of the United States (see review in Boyer and Zedler 1998). Phosphorus was added as triple superphosphate (18% P by mass; 1.5 g $P/m^2/2wk$). The N:P ratio (10:1 by mass) was chosen to mimic that typical of temperate estuarine water (Nixon et al. 1986, Sfriso et al. 1992, Eyre and Balls 1999, K. Boyle unpublished data). The N+P treatment consisted of the two single nutrient doses mixed together. The dry fertilizer was hand-broadcast every two weeks from the boardwalk at low tide (when sediments were exposed), from mid-June 1997 until late July 1998.

Sampling was performed quarterly from June 1997 through August 1998 (June 11 and September 4, 1997; January 7, April 27, and August 12, 1998) at low tide during neap tide series. On each date, sampling was performed within a single quadrant of the plots; the center of each plot was sampled on the fifth and final sampling date. To estimate *S. virginica* biomass, all aboveground vegetation was clipped within a 19.1-cm-diameter sampling cylinder. Aboveground tissues of *S. virginica* were rinsed and divided into ‘‘succulent’’

and ''woody'' stem tissue. Succulent tissue was defined as the young, green or reddish fleshy stems (cortex tissue, enclosed cork layer, and vascular cylinder), while woody stem tissue was older, with an expanded cork layer and thickened vascular cylinder over which the fleshy cortex had senesced and shed (Fahn and Arzee 1959). Tissues were divided in this manner to help discern seasonal patterns in tissue nutrient distribution or biomass. As the succulent tissue senesces, it becomes part of the woody tissue compartment; consequently, changes related to treatment were expected to be found in the succulent portion of tissue first. Tissues were dried at 60°C to a constant mass before weighing and grinding with a Wiley mill to pass through a 40-mesh sieve. Total N (by Kjeldahl procedure, TKN) and total P (by microwave acid digestion) were determined for each tissue component (DANR Analytical Laboratory, University of California, Davis). Due to an oven malfunction, woody stem samples from June 1997 were not analyzed for nutrient content.

The sampling cylinder was also used to remove a core of soil and roots to a depth of 15 cm below the soil surface. From each core, a subsample of live (intact, turgid) roots was removed (non-quantitatively). Root tissue was washed thoroughly over a 0.5-mm sieve, dried, ground, and analyzed for nutrient content as above.

Occasionally there was not enough biomass of above- or belowground tissues to perform nutrient analyses on all samples. Replication is noted in Results; it was never less than n = 3.

In addition, a 2.5-cm-diameter x 10-cm-long soil core was extracted for soil analyses. Soil samples were dried at 60°C, ground, and analyzed for TKN and total P (DANR Analytical Laboratory, University of California, Davis). This study focused on total (inorganic and organic) N and P as an indication of the pool of nutrients potentially available to plants. In addition, on the last sampling date, NH_4-N and NO_3-N were measured on dry soils using KCl extraction (DANR Analytical Laboratory, University of California, Davis).

Final sampling in August 1998 included additional measures. Percent cover of *S. virginica* was estimated using a Plexiglas frame (0.5m x 0.5m) with holes cut to hold a laser pointer. The laser pointer projected a red dot onto the vegetation directly below; the category of cover (succulent, woody, or bare space) was recorded and the pointer moved to the next position, for a total of 36 evenly distributed grid points.

On this last sampling date, the number of branches was counted from each of the biomass samples, and the total number of branches per m^2 was estimated. The number of branches bearing at least one flower was also recorded.

Table 1. Seasonal patterns in sediment total Kjeldahl N (TKN) and total P in control plots (not fertilized). Values are means for 5 plots ± 1 SE. ANOVA summaries appear below each column. Letters indicate *post hoc* comparisons (Fisher's PLSD) following a significant ANOVA; means sharing a letter do not differ.

Date (mo/yr)	TKN (% dry mass)	Total P (% dry mass)
6/97	0.32 ± 0.02[b]	0.14 ± 0.00
9/97	0.25 ± 0.01[a]	0.14 ± 0.01
1/98	0.34 ± 0.02[b]	0.15 ± 0.01
4/98	0.34 ± 0.01[b]	0.14 ± 0.01
8/98	0.36 ± 0.02[b]	0.14 ± 0.00
$F_{4,20}$	6.99	0.17
P	0.0011	0.9492

Also during the last sampling event, belowground tissue mass was sampled quantitatively using a 10-cm-long, 19.1-cm-diameter core. The core extracted from each plot was divided into 0–5 cm and 5–10 cm depth samples and returned to the lab. Soil was rinsed from belowground live and dead tissues (not separated) over a 0.25-mm sieve. Tissues were dried at 60°C, weighed, ground, and analyzed as above.

Seasonal patterns in *S. virginica* biomass, tissue nutrient levels, and soil nutrient levels in the non-fertilized control plots were analyzed with 1-factor ANOVA (factor = sampling date). Analyses for the nutrient addition experiment also employed 1-factor ANOVA (factor = nutrient treatment). One N treatment plot was dropped from analyses on the April and August 1998 data; this plot developed standing water in March 1998 and could no longer be considered a replicate. To meet the assumptions of parametric statistics, the data on flowering were log-transformed. Results were considered significant if $P < 0.05$; however, all ANOVA P values < 0.10 are reported in the Results. If an ANOVA detected significant differences, Fisher's Protected Least Significant Differences (PLSD) tests were used to determine pairwise differences among means; these results are indicated in the tables and figures. SuperANOVA (version 1.11 for MacIntosh) was used for all analyses. All errors presented are ± 1 SE.

RESULTS

Patterns without Nutrient Additions

Sediments. In the control plots, sediment TKN remained constant at ~0.34% dry mass during the study, except for a decrease in September 1997 when TKN was significantly lower (Table 1). Total P in sediments was ~0.14% dry mass during the study, with no significant differences seasonally (Table 1). Total P val-

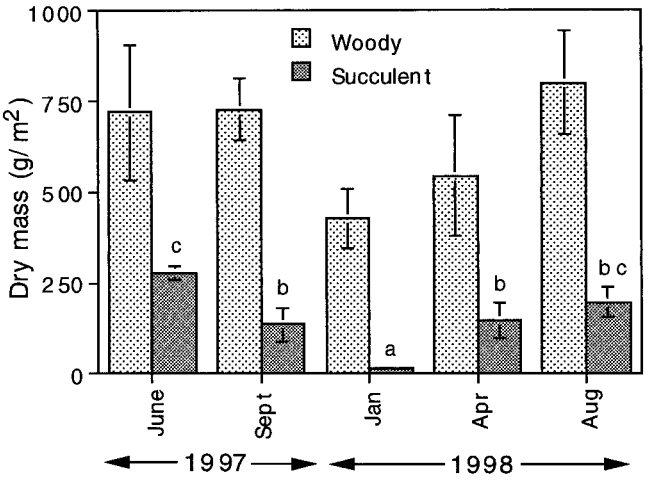


Figure 1. Seasonal changes in distribution of *Salicornia virginica* aboveground biomass in woody stem and succulent tissues in the control (not fertilized) plots (means of 5 replicates ± 1 SE). For succulent tissues, means sharing a letter are not significantly different (Fisher's PLSD). Woody tissues did not differ seasonally (ANOVA $P > 0.05$).

ues were about half those of TKN, except in September 1997. Inorganic nutrients, NH_4-N and NO_3-N, were 174.6 ± 20.3 ppm and 2.3 ± 0.8 ppm, respectively, in August 1998, the only date on which they were measured.

Plants. There was a strong seasonal pattern in *Salicornia virginica* aboveground biomass with time (Figure 1). Maximum aboveground mass (~1000 g/m^2) occurred in June with ~250 g/m^2 of succulent tissue and ~750 g/m^2 of woody stem tissue (Figure 1). Total aboveground mass was ~2x greater in summer (~1000 g/m^2) than in winter (~500 g/m^2). Succulent tissue mass was lower in January than any other month ($F_{4,20} = 6.92$, $P = 0.0011$; Figure 1) and about 10x lower (3% of the total aboveground mass) than in the summer months (20–40% of the total). While woody stem mass seemed to be lowest in January (Figure 1), there were no significant differences by sampling date.

Percent cover was quite high when measured in August 1998 (only date). Total cover in the control plots (no nutrients added) averaged 88 ± 5%, and cover of succulent tissue averaged 34 ± 5%.

Levels of N and P in both succulent and woody aboveground tissues were highest in January and lower through spring and summer (Table 2), suggesting accumulation of nutrients in winter and dilution in tissues during the active growing season. For both N and P, this pattern was more evident in the succulent tissues than in the woody stems. For example, P levels in succulent tissue were 2x greater in January than in August or September, while woody tissues showed a less dramatic (but still highly significant) increase in January (Table 2). Succulent tissue, with less structural material than the woody stems, would be expected to have a greater nutrient content per unit of dry mass.

The N:P ratios (on % dry mass) averaged ~10:1 throughout the year (Table 2). The N:P ratio in succulent tissues was lower in January than in any other month (Table 2), when P levels had increased relatively more than N levels. The woody stem N:P ratio was similar in September 1997 and January 1998, gradually increasing through April and August 1998 (Table 2).

Effects of Nutrient Additions

Sediments. After fertilization for ~14 months (August 1998), N addition seemed to increase NH_4-N levels and decrease nitrate levels relative to controls (Table 3), but differences were not significant. Soil TKN never differed among treatments during the study (e.g., August 1998 data in Table 3). Soil total P showed treatment differences in August 1998 (Table 3); P levels increased significantly only when both P and N were added (see Table 3 for PLSD results).

Plants—Nitrogen Effects. During the fall and winter sampling periods after fertilization began (September 1997 and January 1998), there was no evidence of a N effect on plant characteristics. However, by April 1998 (~11 months after fertilization began), the mass of succulent tissue had increased significantly with N addition ($F_{3,15} = 4.26$, $P = 0.023$; Figure 2a). By August, N amendments led to a doubling of succulent tissue biomass ($F_{3,15} = 17.11$, $P = 0.0001$; Figure 2a). There were no significant treatment effects on woody stem tissue in April or August (Figure 2b); however, there was a trend toward N addition increasing woody stem mass in August ($F_{3,15} = 3.27$, $P = 0.0506$).

In April, N addition tended to increase the N concentration of succulent tissues, but the effect was not significant ($F_{3,15} = 2.62$, $P = 0.089$; Figure 3a); there was no effect on woody stem tissues (Figure 3b). Addition of N seemed to decrease P content of woody stems ($F_{3,15} = 5.20$, $P = 0.0116$); however, the PLSD indicates that this effect was not strong (Figure 3d).

In August 1998, N addition led to increased N content of woody stems ($F_{3,15} = 13.30$, $P = 0.0002$) but did not influence succulent tissues (Figure 3a and b). As in April, added N led to a decrease in P content, this time significantly in both succulent ($F_{3,15} = 7.90$, $P = 0.0022$) and woody tissues ($F_{3,15} = 11.09$, $P = 0.0004$) (Figure 3c and d).

By the end of the study in August 1998, N addition resulted in 2x greater *S. virginica* branching than the control or P addition treatments ($F_{3,15} = 9.65$, $P = 0.0009$; Figure 4a). Increases in biomass seem to have

Table 2. Seasonal patterns in *Salicornia virginica* N, P, and N:P ratios (by mass) in control plots. Values are mean (± 1 SE). Biomass was insufficient to analyze all samples in September 1997 (n = 4 for woody) and January 1998 (n = 3 for succulent); otherwise, n = 5. June 1997 woody samples were not analyzed (see Methods). ANOVA summaries appear below each column; means sharing a letter within a column are not significantly different (Fisher's PLSD).

Date	Total N (% dry mass)		Total P (% dry mass)		N:P Ratio	
mo/yr	Succulent	Woody	Succulent	Woody	Succulent	Woody
6/97	1.80 (0.09)^{bc}	— (—)	0.16 (0.01)^{ab}	— (—)	11.0 (0.3)^{b}	— (—)
9/97	1.57 (0.07)^{a}	1.23 (0.03)^{a}	0.15 (0.01)^{a}	0.13 (0.01)^{b}	10.8 (0.6)^{b}	9.6 (0.5)^{a}
1/98	2.28 (0.02)^{d}	1.64 (0.04)^{c}	0.30 (0.02)^{c}	0.17 (0.01)^{c}	7.7 (0.4)^{a}	9.6 (0.4)^{a}
4/98	1.88 (0.10)^{c}	1.41 (0.07)^{b}	0.18 (0.01)^{b}	0.13 (0.00)^{b}	10.4 (0.5)^{b}	11.3 (0.8)^{ab}
8/98	1.61 (0.05)^{ab}	1.15 (0.03)^{a}	0.15 (0.01)^{a}	0.10 (0.01)^{a}	10.6 (0.4)^{b}	11.9 (0.7)^{b}
df	4, 18	3, 15	4, 18	3, 15	4, 18	3, 15
F	9.89	20.86	31.85	24.26	5.62	3.55
P	0.0002	0.0001	0.0001	0.0001	0.0041	0.0401

been directly related to increased branching (compare Figure 4a to Figure 2).

Nitrogen addition tended to increase the number of flowering branches, but differences were obscured by high variability (Figure 4b). Flower production was proportional to branching; the fraction of branches that bore flowers was similar by treatment.

Despite large increases in branching and biomass with N addition, measures of percent cover did not detect any nutrient effects on the vegetation. Neither total cover nor the succulent or woody portions alone showed treatment effects (Figure 4c).

Addition of N had no effect on nutrient levels in root tissues on any date or on belowground tissue biomass collected at the end of the experiment.

Plants—Phosphorus Effects. Addition of P had no effect on biomass of aboveground or belowground tissues in this study (e.g., April and August 1998 data in Figure 2). However, adding P did affect tissue nutrient concentrations. In August 1998, P fertilization led to significant increases in P content of woody aboveground tissues ($F_{3,15}$ = 11.09, P = 0.0004), although not succulent tissues (Figure 3c and d). There was a similar trend during the previous April of P addition increasing succulent P content ($F_{3,15}$ = 2.61, P = 0.0898; Figure 3c).

Root tissues were also affected by P addition. In September 1997 (after 3 months of fertilization), P addition produced a non-significant increase of both P ($F_{3,13}$ = 2.83, P = 0.0796) and N ($F_{3,13}$ = 2.70, P = 0.0888; Figure 5a and b). In August 1998, P additions had a positive effect on P content of belowground tissues in the top 5 cm ($F_{3,15}$ = 5.04, P = 0.0130; Figure 5d), although not at the 5–10 cm depth (data not shown). No effects of P on root N content were detected in August (Figure 5c).

Plants—Nitrogen + Phosphorus Effects. In this experiment, we typically found only one nutrient to affect a given response variable; the influence of this nutrient remained the same regardless of the addition of the second nutrient. However, there were a few exceptions to this pattern. Alone, P increased woody tissue P content in August, while N decreased P content. When both nutrients were added, the depressive effect of N was dominant, and P levels were significantly lower than when P alone was added (see PLSD results

Table 3. Total Kjeldahl N (TKN), total P, NH_4-N, and NO_3-N in sediments by treatment, August 1998. Plots were either not fertilized (controls = C) or fertilized with nitrogen (N), phosphorus (P), or both (N + P). Values are means ± 1 SE; n = 5 except in the N treatment (n = 4; see Methods). ANOVA summaries appear below each column. Letters indicate *post hoc* comparisons (Fisher's PLSD) following a significant ANOVA; means sharing a letter do not differ.

Treatment	TKN (% dry mass)	Total P (% dry mass)	NH_4 (ppm)	NO_3 (ppm)
C	0.36 ± 0.02	0.14 ± 0.00^{a}	174.6 ± 20.3	2.3 ± 0.8
N	0.33 ± 0.01	0.15 ± 0.01^{a}	214.3 ± 14.6	1.4 ± 1.0
P	0.34 ± 0.01	0.17 ± 0.01^{ab}	153.6 ± 14.3	2.6 ± 0.8
N + P	0.33 ± 0.02	0.19 ± 0.01^{b}	185.4 ± 13.6	1.6 ± 0.4
$F_{3,15}$	0.88	4.44	2.28	0.61
P	0.4753	0.0202	0.1209	0.6191

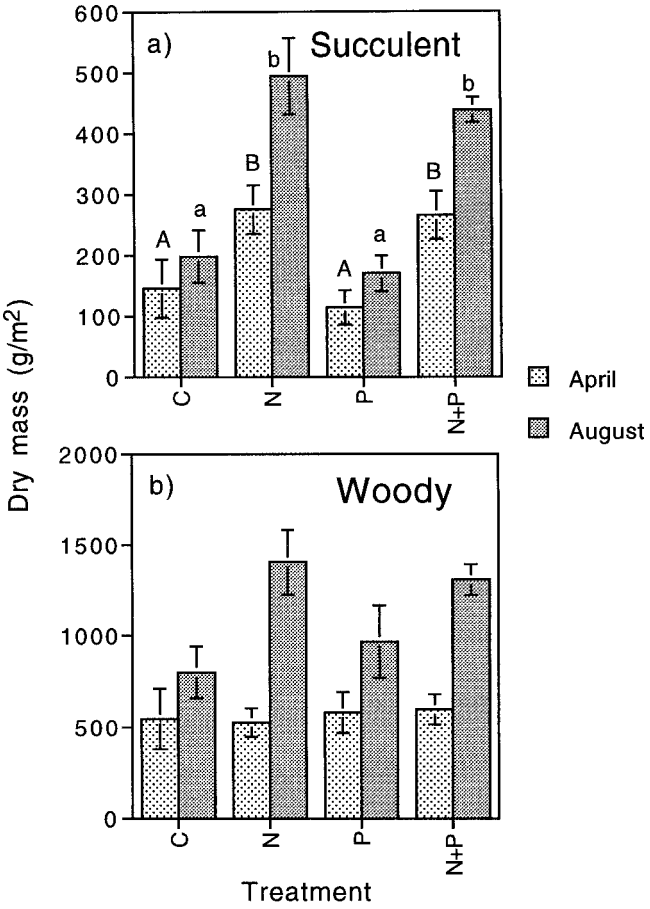


Figure 2. Mass of *Salicornia virginica* succulent (a) and woody stem tissues (b) after ~11 months (April 1998) and ~14 months of fertilization (August 1998) with N, P, both (N+P), or neither (control = C). Error bars are ± 1 SE; n = 5 except in the N treatment (n = 4; see Methods). For succulent tissues, means sharing a letter (uppercase = April, lowercase = August) are not significantly different (Fisher's PLSD). Woody tissues did not differ by treatment (ANOVA $P > 0.05$).

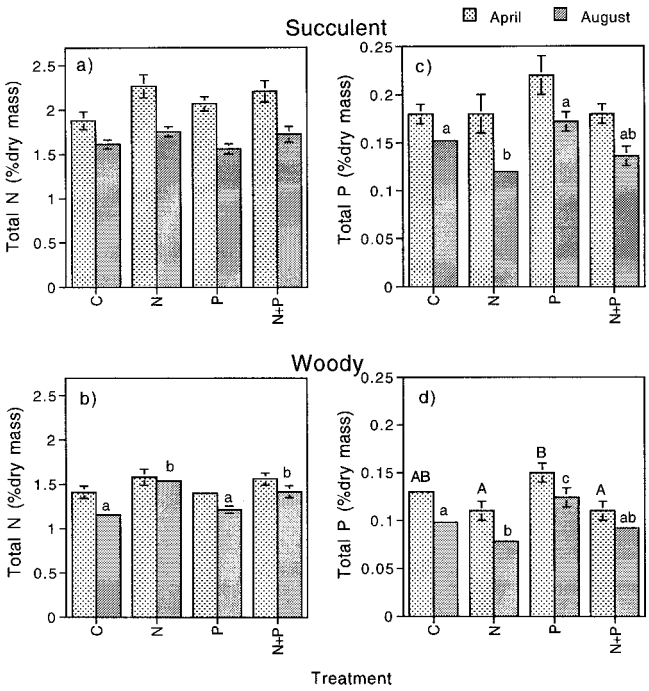
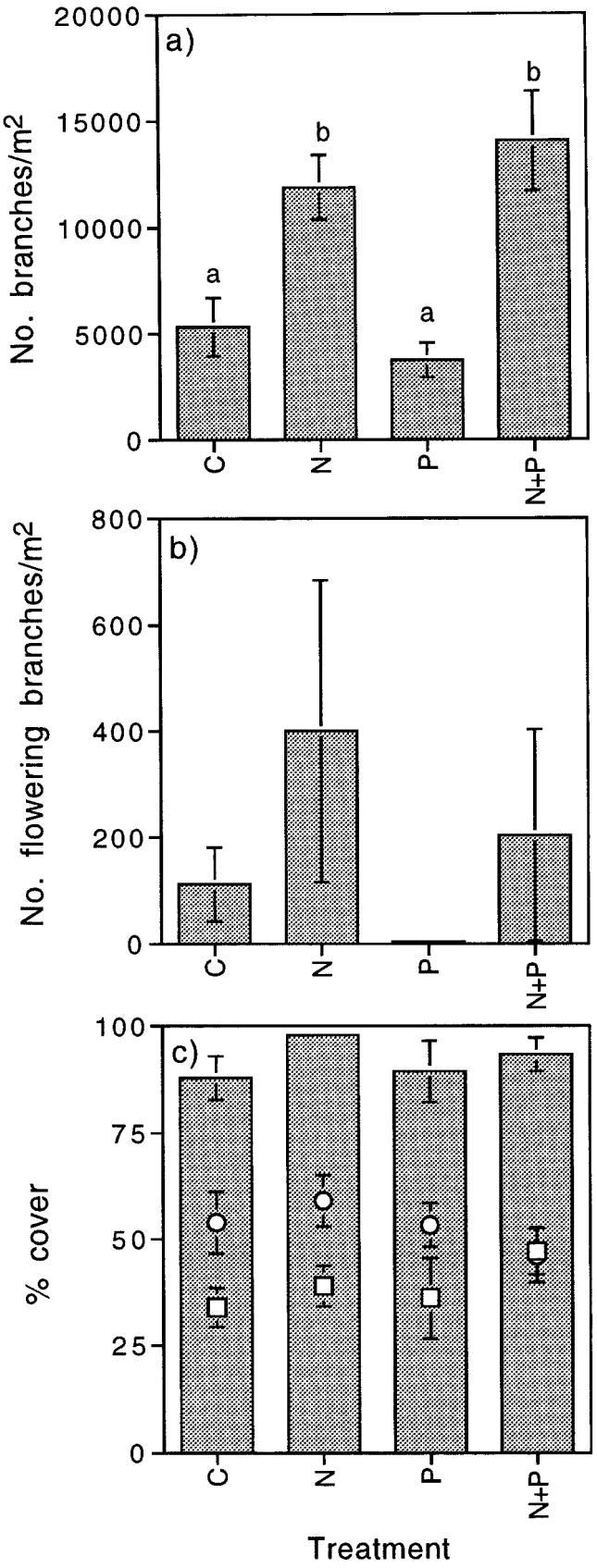


Figure 3. Total N (a and b) and total P (c and d) in the succulent and woody tissues of *Salicornia virginica,* April and August 1998, with additions of N, P, both (N+P), or neither (control = C). Error bars are ± 1 SE; n = 5 except in the N treatment (n = 4; see Methods). Absent error bars are too small to be visible. Means sharing a letter (uppercase = April, lowercase = August) are not significantly different (Fisher's PLSD). Bars without letters indicate ANOVA $P > 0.05$.

in Figure 3d). Another exception was found with root P, which increased significantly only when both N and P were added; however, this effect was not significantly greater than the response to P alone (see PLSD results in Figure 5d).

Plants—N:P Ratios. While N levels in succulent tissues increased during winter, P levels increased relatively more, causing a drop in N:P ratios in all treatments (Figure 6a). Nitrogen addition began to increase tissue N:P ratios in succulent tissues relative to the other treatments as early as January 1998 ($F_{3,9} = 5.19$, $P = 0.0236$; Figure 6a). This effect continued in April ($F_{3,15} = 3.53$, $P = 0.0409$; Figure 6a), and by August 1998, N:P ratios had reached 14.6 ± 0.5 in N addition plots compared to 10.6 ± 0.4 in the unfertilized controls ($F_{3,15} = 19.70$, $P = 0.0001$; Figure 6a). Addition of P produced a non-significant decline in N:P ratios by August 1998 (Figure 6a). When both nutrients were added, this negative effect of P brought the N:P ratio significantly lower than when only N was added (Figure 6a).

As in the succulent tissues, N:P ratios of woody tissues (Figure 6b) increased with N addition beginning in January 1998 ($F_{3,16} = 4.71$, $P = 0.0154$). This trend continued in April ($F_{3,15} = 7.91$, $P = 0.0021$), and by August 1998, N:P ratios had increased dramatically with N addition ($F_{3,15} = 46.23$, $P = 0.0001$; Figure 6b). This effect was largely due to a decrease in total P in all the treatments at that time. For example, P levels in the +N treatment decreased from 0.11 to 0.08% of dry mass from April to August (Figure 3d), while N levels decreased relatively less (from 1.58 to 1.54% N) for the same period (Figure 3b). As in the succulent tissues, P addition led to a decrease in woody stem N:P ratios in August 1998 and also reduced the positive effect of N when both nutrients were added together (see PLSD results in Figure 6b).



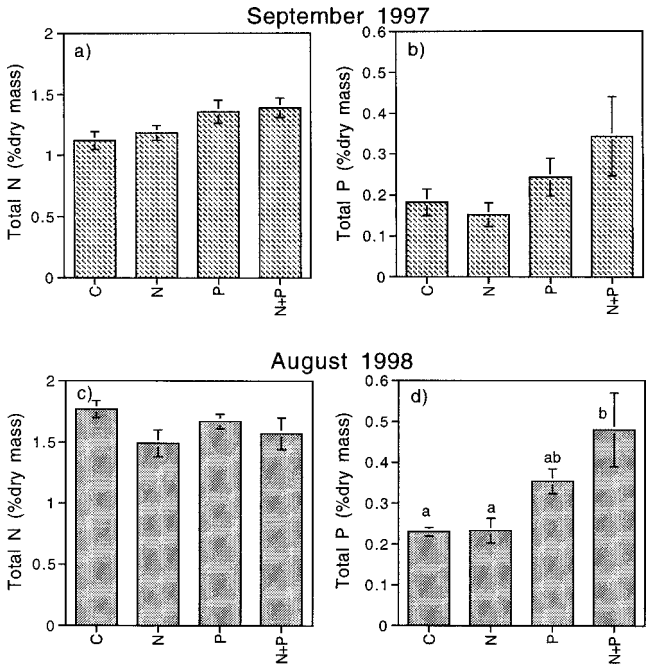


Figure 5. Total N (a) and total P (b) in live root tissues (sample haphazardly removed from a 15-cm deep core) after 3 months of fertilization (September 1997) with N, P, both (N+P), or neither (control = C). Total N (c) and total P (d) in belowground tissues (live + dead total mass in 5-cm deep core) after ~14 months of fertilization (August 1998). Error bars are ± 1 SE. In September 1997, n = 5 except in the P (n = 4) and N+P (n = 3) treatments, where biomass was insufficient to analyze all samples. In August, n = 5 except in the N treatment (n = 4; see Methods). In (d), means sharing a letter are not significantly different (Fisher's PLSD). Elsewhere, bars without letters indicate ANOVA $P > 0.05$.

DISCUSSION

Sediment Characteristics

Our sediment total N levels (0.32% annual mean) were moderate compared to other US east, gulf, and northwest coast studies but higher than in other southern California marshes. Sediment total N in natural, lower elevation salt marshes of the US east and gulf coasts (dominated by *Spartina alterniflora*), ranged

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Figure 4. Total number of branches (a), number of branches bearing at least one flower (b), and percent cover (c) in August 1998, with additions of N, P, both (N+P), or neither (control = C). In (c), bars = total, squares = succulent tissues only, and circles = woody tissues only. Error bars are ± 1 SE; n = 5 except in the N treatment (n = 4; see Methods). In (a), means sharing a letter are not significantly different (Fisher's PLSD). Elsewhere, bars and symbols without letters indicate ANOVA $P > 0.05$.

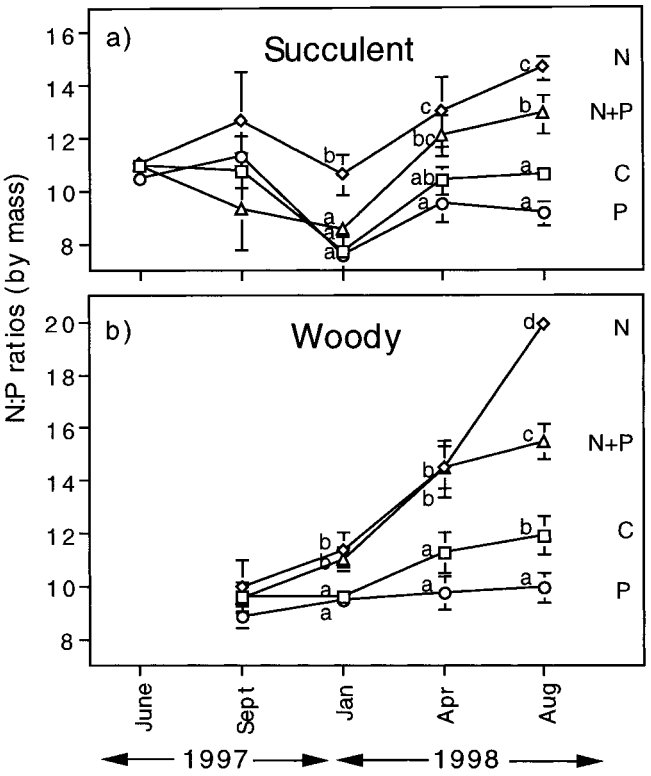

Figure 6. N:P ratios (by mass) of succulent (a) and woody tissues (b) with additions of N, P, both (N+P), or neither (control = C) during the study. Error bars are ± 1 SE; n = 5 except in succulent tissues in January 1998 (n = 3, 4, 3, and 4 in the C, N, P, and N+P treatments, respectively, due to insufficient biomass for nutrient analysis) and in April and August 1998 (n = 4 for the N treatment; see Methods). June 1997 woody samples were not analyzed (see Methods). For each date, means sharing a letter are not significantly different (Fisher's PLSD). Dates for which symbols have no letters indicate ANOVA $P > 0.05$.

from ≤0.09% (Lindau and Hossner 1981, Craft et al. 1999) to about 0.8% (Buresh et al. 1980, Ellison et al. 1986), with most in the 0.4–0.8% range (Mendelssohn and Marcellus 1976, Wetzel and Powers 1978, Buresh et al. 1980, DeLaune and Pezeski 1988, Craft et al. 1999) and a few in the 0.2–0.35% range (Mendelssohn and Marcellus 1976, Chalmers 1979, Haines 1979).

Few N data are available for sediments from marshes of the US west coast. Seliskar (1985) found 0.62% N in *S. virginica*-dominated marsh areas in Oregon, about 2x higher than in the current study at Mugu Lagoon. In southern California marshes, only data for *S. foliosa*-dominated marshes are available for the lower elevations. Nitrogen levels in this study are higher than those found in a natural marsh on San Diego Bay (0.17–0.20%) (Langis et al. 1991, Boyer and Zedler 1998), ~230 km SE of Mugu Lagoon. While we measured extractable inorganic nutrients only in August 1998, NH_4-N values were more than 40x greater and NO_3-N values 10x greater than in the San Diego Bay study (~4 ppm and ~0.22 ppm, respectively, sampled in April and May, Langis et al. 1991). Inorganic N (NH_4-N + NO_3-N) in this study also greatly exceeded levels found in Tijuana Estuary (6.6 ppm total inorganic N; Covin and Zedler 1988), ~240 km SE of Mugu Lagoon.

Sediment P levels were much higher at Mugu Lagoon (~0.14%) than in natural *S. alterniflora* marshes of the US east and gulf coasts, from which literature values range between 0.01 and 0.09% (Mendelssohn and Marcellus 1976, Ellison et al. 1986, DeLaune and Pezeski 1988, Craft et al. 1999). We know of no other sediment P data from low to mid-elevation, vegetated marshes of southern California or elsewhere on the US west coast.

In general, sediment N levels in this study were high compared to levels in other southern California marshes but moderate compared to levels in other US marshes; our sediment P levels were high relative to all other low to mid-elevation marshes for which data were available. While little water nutrient sampling has been performed at Mugu Lagoon (T. Keeney, NBVC, unpublished data), soil nutrient levels suggest that watershed nutrient inputs have been high. The Calleguas Creek watershed draining into Mugu Lagoon contains agricultural, residential, and light industrial sectors, and runoff contains high concentrations of fertilizers. Virtually all the runoff during the dry season (~March–October) is irrigation waste or treated wastewater. At least one large sewage spill (315 million liters over 2–3 weeks) has entered Calleguas Creek in recent years (California Regional Water Quality Control Board, unpublished data). In addition to the water-borne nutrient supply, shallow waters and sediment surfaces exposed at low tide can receive direct dry deposition of atmospheric nutrients, exacerbating eutrophic conditions (Paerl 1993, 1995). In southern California, dry deposition of N can be substantial near urban areas in summer (R. Lu and R. Turco, UCLA Department of Atmospheric Sciences, unpublished manuscript).

Plant Characteristics

There are few studies in the literature that report *S. virginica* biomass. We measured much greater aboveground biomass during the growing season than Page (1995) did at Carpinteria Marsh (12 km E of Santa Barbara, CA). In that study, mass ranged from 108 to 401 g/m^2 in varying locations and months (March–August). In contrast, we found similar or slightly lower values than Covin and Zedler (1988) at Tijuana Estuary (1316 g/m^2). In northern California (San Francisco Bay), Mahall and Park (1976) found higher aboveground biomass (maximum: 2722 g/m^2; mean: 1468–1885 g/m^2), but Zhang et al. (1997) found sim-

ilar values of 1100–1300 g/m^2 at San Pablo Bay (in the northern reaches of San Francisco Bay). Kennedy and Brink (1986) found ~1400–2000 g/m^2 on Vancouver Island, British Columbia (May–August). Compared to these other marshes, this portion of Mugu Lagoon marsh seems to support an intermediate biomass of *S. virginica*. Within Mugu Lagoon marshes, our study found much higher biomass than Onuf (1987), who measured 250–750 g/m^2 during the growing season at varying locations over several years. High spatial and interannual variability seem to be common for this species, making comparisons of biomass both within and between marshes problematic. This variability is suggested by the wide ranges in biomass in the studies above; furthermore, at Mugu Lagoon, previous work has found sampling stations to vary in *S. virginica* biomass by as much as 500 g/m^2 from year to year (Onuf 1987).

The mean N:P ratio of both succulent and woody tissue was ~10:1 (by mass) on average in the unfertilized control plots but dropped in winter to 7.6:1 in succulent tissues. Others have used N:P ratios to examine seasonal changes in nutrient limitation in macroalgae (Wheeler and Björnsäter 1992). If we were to apply this concept to the decreasing N:P in winter found in our succulent tissue data, we might conclude that N is more limiting and P less limiting in winter than in other seasons. However, tissue N concentration was also high in winter but simply did not increase as much as P did relative to other seasons. Further complicating interpretation, N:P ratios in the woody stems did not exhibit the same decline in winter as did succulent tissues. Clearly, it is difficult to interpret N:P ratios without also examining the underlying patterns in nutrient concentrations.

Patterns with Nutrient Additions

Despite high sediment N levels in this *Salicornia virginica* marsh at Mugu Lagoon, N additions for >1 year led to large increases in succulent tissue biomass, the degree of branching, N content, and N:P ratios of aboveground tissues. In agreement with work at Tijuana Estuary (Covin and Zedler 1988), this study provides strong evidence that *S. virginica* is limited by N at Mugu Lagoon.

While there were no significant increases in the mass of the older, woody tissues with N addition during the study, there were large increases in new growth, the succulent tissues. A later sampling date in the fall or winter of 1998, after senescence and shedding of the fleshy outer tissues, would likely have detected a delayed response to N addition as increased woody stem biomass. A non-significant trend in August 1998 suggests that N-enhanced succulent biomass was beginning to ''become'' woody stem biomass (see Figure 2b).

Nitrogen addition led to a decrease in tissue P content in both succulent and woody tissues in August 1998, reflecting the growth response of the plants. With N addition, new growth (succulent tissue) increased in April and doubled by August. Growth of these tissues must have had a dilution effect on P concentration. This effect was ameliorated somewhat by the addition of P along with N.

Even though sediments were high in total P, adding P fertilizer enhanced *S. virginica* tissue P levels. Specifically, P fertilization led to increased P content of woody stem tissues in August 1998. Further, adding P increased root P levels late in the growing season (a trend in September 1997 and a significant effect in August 1998). While we did not detect effects of P on other plant characteristics, uptake and storage of P in the tissues is suggestive of P demand in this stand of *S. virginica.*

As with examining seasonal trends, N:P ratios have been used to assess nutrient demand of macrophytes under different environmental conditions (Atkinson and Smith 1983, Shaver and Melillo 1984, Osgood and Zieman 1993). In our study, large increases in tissue N:P ratios with N addition suggest that if N inputs to *S. virginica* marshes increase without P inputs also increasing, then P may become the more limiting nutrient.

Percent cover sampled at the experiment's end showed no patterns with nutrient addition treatment, despite large differences detected by biomass and branching measures. Percent cover can be a useful, non-destructive indicator of changes in vegetation patterns (e.g., in Callaway and Pennings 1998). However, in this study, initial plant cover was very high (~90%), and the main response was, in effect, increased canopy layering and probably also height (pers. obs.). Cover measurements are not appropriate for detecting changes of this kind.

Effects of Other Edaphic Factors

Plant nutrient uptake and use may depend, in part, on soil salinity. While soil salinities were not measured in the field at this site, saturated soil pastes (Richards 1954) performed *post hoc* on dried soil samples (from June 1997) detected very high salinity levels (mean of 20 samples = 75.5 $\pm$ 2.1 ppt). Moisture levels may be up to 34% lower in saturated pastes than in the field (A. Armitage unpublished data); to be conservative, a downward adjustment of paste salinities by 40% yields a mean of 47 $\pm$ 1.3 ppt. Even this conservative estimate of field salinities suggests that plants are growing in hypersaline conditions.

Numerous studies of *Spartina alterniflora* marshes have found that elevated soil salinities diminish productivity, probably due to negative effects of osmotic stress on root functioning or through competitive exclusion of ammonium ions by excess sodium ions (Haines and Dunn 1976, Bradley and Morris 1991, Osgood and Zieman 1993). Further, high soil salinity may cause increased N demand to counter osmotic stress, as osmotica such as proline and glycine-betaine contain N (Cavalieri and Huang 1979, 1981). Hence, salt-stressed plants may respond to increased N supply by increasing N content, but not by growing (Bradley and Morris 1992). We would expect such plants to grow poorly, or not at all, in response to added N. However, despite the high soil salinities estimated in this study, *S. virginica* not only increased its N concentration with N addition, but it also greatly increased its biomass. High salinities are typical in Mediterranean-type climates where precipitation is low, temperatures warm, and evaporation high (Callaway et al. 1997, Haltiner et al. 1997); plants growing in such conditions may be well-adapted to hypersaline soils.

It is possible that other edaphic factors limit availability of N to plants in this salt marsh and that our fertilizer additions ameliorated the limiting conditions. One study found N addition to reduce both temperature and salinity stress of *Spartina alterniflora* (Shea et al. 1975). Plant mineral nutrition and nutrient availability are related to many other characteristics of soils that were not assessed in this study, such as pH, redox potential, hydrogen sulfide levels, and decomposition processes (Howes et al. 1981, Tisdale et. al 1985, Bradley and Morris 1990, Koch et al. 1990).

Implications for Community Processes

This study suggests that seasonal losses of *S. virginica* biomass may contribute substantially to the pool of detrital carbon and nitrogen at Mugu Lagoon. From September 1997 to January 1998, about half of the total biomass was shed (see Figure 1), or about 420 g/m^2. This loss equates to >4000 kg/ha, a significant amount considering *S. virginica*'s areal extent at Mugu Lagoon. Food web analyses using stable isotopes have found that *S. virginica* is an important food source for marsh detritivores, although channel-dwelling organisms rely more on algae for food (Kwak and Zedler 1997, Page 1997). Additions of organic matter and nutrients to sediments through biomass losses may enhance plant nutrition in vegetated areas and may help to build soils for future plant establishment.

Although not measured in this study, we hypothesize that increased N enrichment may lead to even greater contributions of biomass, and perhaps nutrients, to the detrital pool in winter. Our N additions resulted in >2-fold increases in *S. virginica* biomass during the growing season (see Figure 2), presumably increasing biomass losses during winter, too. Nitrogen concentrations also increased, but we lack data on *S. virginica*'s efficiency in retranslocating nutrients to roots at senescence, so we cannot speculate on N mass contributed to the detritus. Increased (and perhaps N-enriched) quantities of detritus would likely influence other salt marsh or estuarine community functions.

As the highest N and P levels in tissues were found in winter when overall biomass (and especially the photosynthetic succulent tissue) was low, *S. virginica* must have some ability to sequester and store nutrients for later use. However, our additions of N and P had no effect on tissue nutrient levels in winter, suggesting that luxury uptake is limited during that time. While wetland plants are generally thought to act as ''filters'' of nutrients from the surrounding watershed, this effect may be limited to the active growing season. As runoff during storms is greatest in the winter months in California, salt marshes dominated by *S. virginica* may not be effective at buffering coastal waters from nutrients.

Even though our study site had relatively high sediment nutrient concentrations, increases in nutrient availability, especially N, greatly affected *S. virginica* characteristics. Canopy architecture was visibly altered where N was added, with numbers of branches increasing by 100% over control plots. Previous work has found that nutrient inputs can shift species composition in salt marshes, favoring *Salicornia* species over others (Covin and Zedler 1988, Boyer and Zedler 1999, K. Boyer and A. Armitage unpublished data). This study suggests that *S. virginica*'s increased canopy density in response to N may be a mechanism for competitive exclusion of other plant species. Further, *S. virginica*'s growth habit may enhance its success through periods of lower N availability. After succulent tissues shed during senescence, the underlying woody stem tissues remaining in spring should reflect the degree of branching developed during the previous growing season.

ACKNOWLEDGMENTS

This research was supported by the U.S. Environmental Protection Agency under Grant R825381 through the UCLA Institute of the Environment. We thank Steve Lee for helping to set up the experiment and develop sampling methods and Krista Kamer, Risa Cohen, Anna Armitage, Karleen Boyle, Diedre Washington, Shannon Lee, and Jenny Lee for help with field work and sample processing. We thank Tom Keeney and the Naval Base Ventura County for permission to perform this study and for their continued support of wetland research.

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Manuscript received 11 September 2000; revisions received 27 November 2000 and 24 March 2001; accepted 8 May 2001.