

2003

Species-Rich Plantings Increase Biomass and Nitrogen Accumulation in a Wetland Restoration Experiment

John Callaway

University of San Francisco, callaway@usfca.edu

Gary Sullivan

Joy B. Zedler

Follow this and additional works at: <http://repository.usfca.edu/envs>

 Part of the [Environmental Sciences Commons](#)

Recommended Citation

John C. Callaway, Gary Sullivan, and Joy B. Zedler 2003. Species-Rich Plantings Increase Biomass and Nitrogen Accumulation in a Wetland Restoration Experiment. *Ecological Applications* 13:1626–1639.

This Article is brought to you for free and open access by the College of Arts and Sciences at USF Scholarship: a digital repository @ Gleeson Library | Geschke Center. It has been accepted for inclusion in Environmental Science by an authorized administrator of USF Scholarship: a digital repository @ Gleeson Library | Geschke Center. For more information, please contact repository@usfca.edu.

SPECIES-RICH PLANTINGS INCREASE BIOMASS AND NITROGEN ACCUMULATION IN A WETLAND RESTORATION EXPERIMENT

JOHN C. CALLAWAY,^{1,4} GARY SULLIVAN,² AND JOY B. ZEDLER³

¹Department of Environmental Science, University of San Francisco, 2130 Fulton St.,
San Francisco, California 94117 USA

²The Wetlands Initiative, 53 West Jackson Boulevard, Suite 1015, Chicago, Illinois 60604-3703 USA

³Botany Department and Arboretum, 430 Lincoln Drive, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. Our test of the hypothesis that biomass and nitrogen would increase with more species-rich plantings simultaneously vegetated a salt marsh restoration site and demonstrated that on average, randomly chosen, 6-species plantings accumulated more biomass and nitrogen than the mean for 0- and 1-species assemblages, with the mean for 3-species assemblages being intermediate. In addition, we found that individual species (from the pool of eight native halophytes) differed in their functional capacity, with *Salicornia virginica* (Sv) and *Jaumea carnosa* contributing the greatest biomass when planted alone, while *Triglochin concinna* had the highest tissue N concentrations. When planted alone, Sv accumulated comparable amounts of biomass and nitrogen as in the multispecies plots, indicating that individual species can have a large effect on particular functions. Soil TKN in the surface 0–5 cm was greater in 6-species plots than unplanted plots in 1999, while both 3- and 6-species plots were greater than unplanted plots in 2000; however, there were no differences at 5–20 cm depth and no species-specific effects. Root and shoot biomass both increased with species richness, with total biomass of 6-species plots averaging 995.6 ± 120.5 g/m² in 2000, compared to the mean for 1-species plots (572.1 ± 90.3 g/m²) and unplanted plots (164.5 ± 24.7 g/m²). Still, at the age of three years, root biomass was only about one-third that of the species-rich reference site, and shoot biomass was one-half to one-fifth the maxima reported for reference salt marshes. Species-specific effects were found for Sv, which had high biomass of both roots and shoots in the multispecies plots (55% of aboveground biomass in 3-species plots and 41% in 6-species plots) and the highest pool of N (52% of the N pool in 3-species plots and 42% in 6-species plots), even though only one-eighth of the initial plantings were Sv. However, when plots with this species were excluded from the analysis, the species-richness effect persisted. Thus, ecosystem function, as measured by biomass and N accumulation, increased with species richness regardless of dominance by the highly productive Sv. We conclude that manipulating the richness and composition of plantings offers ecosystem restorationists an effective tool for accelerating the rate of functional development.

Key words: biodiversity; diversity; ecosystem functions; nitrogen; richness; *Salicornia virginica*; salt marsh; wetland restoration.

INTRODUCTION

The last decade has seen an explosion of interest in the relationship between species diversity and ecosystem function, with many experiments supporting positive relationships between species richness and productivity, despite controversies over the interpretation of results (Schulze and Mooney 1993, Naeem et al. 1994, Huston 1997, Tilman et al. 1997, 2001, Schwartz et al. 2000, Tilman 2000, Engelhardt and Ritchie 2001). To date, researchers have asked how the loss of species diversity affects ecosystem functioning (Naeem et al. 1994, Chapin et al. 2000, Tilman et al. 2001), focusing on the concern of global impacts to species diversity (Pimm et al. 1995, Gaston 2000). But as natural habitats

continue to be lost, conservationists become increasingly dependent on restoration efforts for improving the status of degraded ecosystems (Daily 1995, Dobson et al. 1997). Hence, we asked a corollary question: Does increasing the number of species accelerate the development of functions in restored ecosystems?

Improving our ability to restore functional ecosystems requires that we identify the factors that constrain ecosystem development (Simenstad and Thom 1996). Attempts to understand natural ecosystem development date to Odum's seminal paper (1969), and the development of ecosystem functions has been linked to the accumulation of soil organic matter (Jenny 1941, Crocker and Major 1955) and the soil nutrient pool (Chapin et al. 1986, Vitousek et al. 1993, Schlesinger et al. 1998, Crews et al. 2001). However, few investigators have followed the cycling and retention of carbon and nutrients in restoration sites over long time periods (Bishel-Machung et al. 1996, Simenstad and

Manuscript received 29 April 2002; revised 18 December 2002; accepted 30 January 2003; final version received 26 February 2003. Corresponding Editor: I. C. Burke.

⁴ E-mail: callaway@usfca.edu

Thom 1996, Craft et al. 1999, Shaffer and Ernst 1999, Zedler and Callaway 1999), and none has linked changes to biodiversity (e.g., the number of species of plants that comprise the vegetation). If it could be demonstrated that organic matter and nutrients accumulate readily in ecosystems restored with certain species or with a diversity of species, then planting protocols could be developed to accelerate the restoration process.

A newly excavated (and bare) restoration site at Tijuana Estuary, southern California, offered the opportunity to test relationships between ecosystem development rates and the composition and the species richness of plantings. The naturally occurring marsh plain community has eight common halophytes (mostly succulents) that are amenable to planting. We hypothesized that the ecosystem would develop more rapidly (i.e., accumulate more biomass and nitrogen) if planted with certain species (such as the regional dominant) or a high initial number of species. We selected N as a focus because salt marshes in this and other regions are known to be N limited (Valiela and Teal 1974, Patrick and DeLaune 1976, Buresh et al. 1980, Covin and Zedler 1988), and N is of special concern for restored and created wetlands (Craft et al. 1988, 1991, Langis et al. 1991, Gibson et al. 1994, Boyer and Zedler 1998). We did not consider tests of functional groups (Hooper and Vitousek 1997, Tilman et al. 1997), because previous greenhouse experiments (Sullivan and Zedler 1999) failed to identify such groupings based on biomass and N retention of these same eight halophytes. Lacking functional groups, we chose to vary species richness, growing species alone and in randomly drawn assemblages. In addition, we were able to explore species-composition effects by subdividing the randomly chosen assemblages into sets with and without the regional dominant, *Salicornia virginica* (Zedler et al. 2001). Being a restoration site, plantings were allowed to change in composition over time via recruitment from seeds that were either produced on site or dispersed naturally (e.g., by the tides).

Specifically, we predicted that (1) soil in unplanted plots would accumulate nitrogen most slowly; (2) *S. virginica* would accumulate more biomass and nitrogen than other species; (3) species-rich plantings would increase the rates of biomass accumulation and N retention; and (4) plots with plantings that rapidly accumulated shoot biomass would suppress the accumulation of biomass contributed by unplanted species. We focused on plant biomass and N concentrations in plant tissues in midwinter, after the growing season had ended and plants were relatively dormant. Winter sampling ensured that storage belowground was maximized, as this community is semidormant during the coldest months (Onuf 1987). In addition, we measured the N content of soil during the growing season and the change in diversity due to recruitment. Related papers from this same experiment explore two additional re-

sponse variables: canopy architecture (Keer and Zedler 2002) and seedling recruitment (Lindig-Cisneros 2001, Lindig-Cisneros and Zedler 2002).

METHODS

Site description

Research was conducted at the Tidal Linkage (Fig. 1), an excavated salt marsh plain within the Tijuana River National Estuarine Research Reserve, hereafter Tijuana Estuary. The Tidal Linkage was designed to add salt marsh habitat and to improve tidal flow by connecting two tidal channels within the north arm of Tijuana Estuary. This 0.7-ha project was the first part of a 200-ha adaptive plan for tidal restoration within the estuary. The area was excavated from disturbed upland in late 1996 and graded in early 1997. We used a 90-m stretch of marsh plain along the tidal channel for our experimental plots (Fig. 1).

Design, site preparation, and planting

In order to evaluate the effect of species richness and compare individual species on ecosystem functions within this newly restored site, we established a series of treatment plots with 0, 1, 3, or 6 plant species. Plants were chosen from a pool of the eight most common marsh plain species in southern California: *Batis maritima* (Bm, perennial trailing succulent), *Frankenia salina* (Fs, perennial upright forb), *Jaumea carnosa* (Jc, perennial trailing succulent), *Limonium californicum* (Lc, perennial basal rosette with taproot), *Salicornia bigelovii* (Sb, annual upright succulent), *Suaeda esterua* (Se, short-lived succulent subshrub), *Salicornia virginica* (Sv, perennial succulent subshrub), and *Triglochin concinna* (Tc, winter ephemeral succulent graminoid). Additional plant attributes appear in Sullivan and Zedler (1999). We established five blocks along the tidal channel (A–E, west to east; Fig. 1) and planted five replicates of each of the 8 species alone (1 replicate/block), and 15 unique combinations of randomly chosen 3- and 6-species assemblages (3 replicates/block; Table 1). In addition, we established 15 plots with no plants (3 replicates/block). One plot each of the most common naturally occurring 3- and 6-species assemblages was also planted (total = 87 plots), but only the 85 randomly selected treatment plots are included as a test of diversity effects.

Plots were 2 × 2 m, spaced 0.75 m apart. A hardpan was ripped up using a track-hoe. Fine sediment was salvaged from the nearby tidal flat, and a thin layer of this sediment was worked into the mineral substrate prior to planting. We rototilled each plot and used hand shovels to homogenize the top 20–25 cm of soil and grade the surface of the plots. Following mixing, each plot surface was smoothed with a hand trowel.

The elevation of each plot was determined with a surveyor-grade autolevel, relative to an adjacent benchmark. The benchmark elevation had been transferred

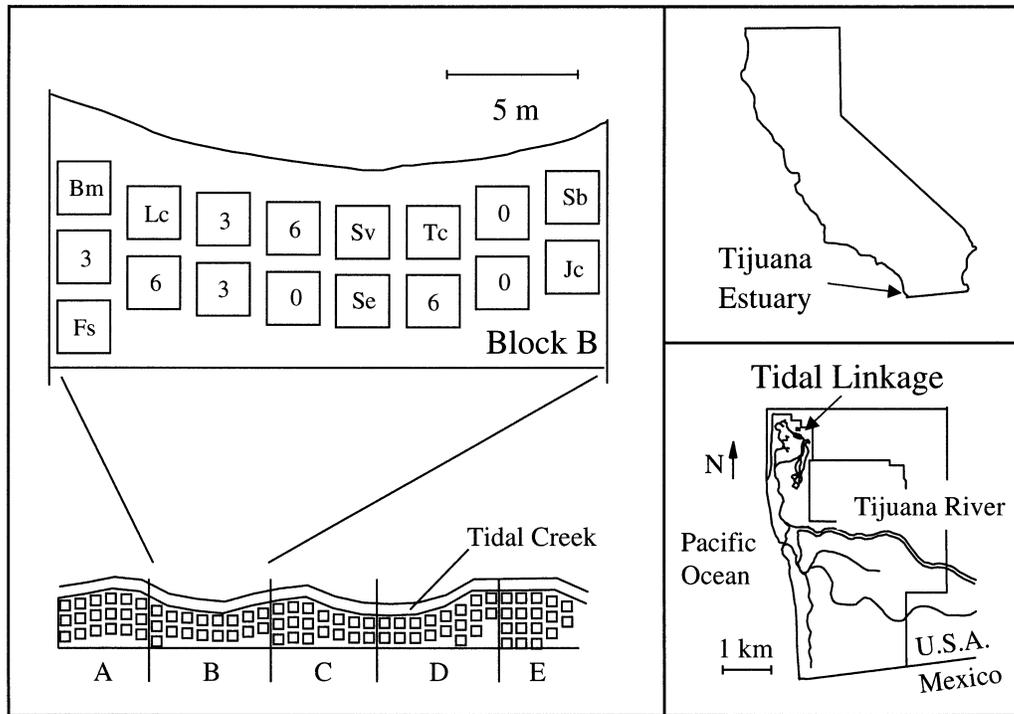


FIG. 1. Location of the Tidal Linkage and the layout of experimental plots. Blocks are indicated, and the random layout of one block is shown. Numbers identify unplanted (0), 3-species, and 6-species plots. Codes indicate the species planted in 1-species plots: Bm = *Batis maritima*, Fs = *Frankenia salina*, Jc = *Jaumea carnosa*, Lc = *Limonium californicum*, Sb = *Salicornia bigelovii*, Se = *Suaeda esteroa*, Sv = *Salicornia virginica*, and Tc = *Triglochin concinna*.

from a USGS certified benchmark within 1000 m of the site using RTK (real-time kinematic) corrected global positioning system equipment (~ 2 cm accuracy). The 85 plots ranged 0.37 m in elevation, from 0.77 to 1.14 m NGVD (National Geodetic Vertical Datum = the 1929 mean sea level). The grand mean elevation was 0.916 ± 0.009 m NGVD, and means for each of the blocks were as follows: (A) 0.859 ± 0.014 m; (B) 0.896 ± 0.18 m; (C) 0.930 ± 0.19 m; (D) 0.904 ± 0.11 m; and (E) 0.992 ± 0.024 m. Mean elevations differed significantly between blocks ($P = 0.001$). However, when both elevation and block were included in analyses of biomass or N, elevation had no effect on ecosystem properties, so elevation was dropped from further analyses.

Locally collected seeds were germinated in December 1996, and seedlings were grown in the greenhouse until they were planted in the field in April 1997. Seedlings were planted in a 9×10 grid with 20-cm spacing between plants, for a total of 90 plants per plot. Multispecies assemblages had 30 individuals of each species (for 3-species plots) or 15 (for 6-species plots) in a repeating pattern that allowed for maximum interaction among species and minimized spatial patchiness within plots. To reduce edge effects, the outer 30-cm border of the plots was avoided during sampling.

We removed "volunteer" seedlings of all species that were not planted in a plot during the first two

growing seasons (1997 and 1998) in order to facilitate growth of planted species (see Keer and Zedler 2002). Using reserved greenhouse-grown seedlings, we replaced transplants that died in 1997 and over the 1997–1998 winter ($<10\%$ in 1997; $<20\%$ in 1998; Zedler et al., *in press*). After two full growing seasons, we allowed recruits to colonize all plots and stopped replacing dead plants (cf. Lindig-Cisneros 2001).

Soil and root sampling

Soil samples were collected in April 1997, August 1999, and August 2000. Samples were collected from eight randomly selected plots within each block in April 1997, and from all plots in 1999 and 2000. On each date, three haphazardly located soil cores (1.75 cm diameter) were collected from a plot and sectioned into 0–5 cm and 5–20 cm depths. Samples from the three cores were composited, dried, ground, and analyzed for N. In 1997 only samples from 0–5 cm were analyzed.

Belowground plant material was collected using soil cores in February–March 1999 and January 2000. Three cores were randomly located within each plot, and belowground samples were collected with a 10 cm diameter coring tube (Hargis and Twilley 1994). Two cores were collected to 18 cm, and only one was collected to 24 cm to reduce impacts to the restoration site. All cores were sectioned into 6-cm intervals in

TABLE 1. Randomly assigned 3- and 6-species assemblages planted at the Tidal Linkage, Tijuana Estuary, California.

Three-species assemblages	Six-species assemblages
Lc Tc Jc	Lc Fs Jc Sb Tc Sv
Tc Se Sv	Jc Se Sb Sv Tc Bm
Sv Fs Bm	Se Fs Lc Tc Sb Jc
Tc Bm Sb	Sb Sv Se Fs Tc Jc
Fs Sv Tc	Fs Sv Sb Jc Bm Lc
Bm Lc Se	Bm Tc Jc Lc Se Sv
Se Sv Jc	Jc Lc Sv Sb Se Bm
Se Sv Fs	Lc Sb Se Tc Sv Fs
Jc Lc Se	Jc Bm Lc Fs Tc Se
Lc Se Tc	Se Sb Sv Bm Fs Lc
Sb Jc Sv	Bm Sb Jc Fs Tc Sv
Tc Sb Jc	Tc Sb Lc Sv Se Jc
Bm Lc Fs	Sv Lc Se Fs Bm Tc
Sv Jc Lc	Tc Bm Lc Fs Jc Sb
Fs Jc Sb	Jc Bm Sv Fs Tc Se

Notes: Bm = *Batis maritima* (perennial trailing succulent), Fs = *Frankenia salina* (perennial upright forb), Jc = *Jaumea carnosa* (perennial trailing succulent), Lc = *Limonium californicum* (perennial basal rosette with taproot), Sb = *Salicornia bigelovii* (annual upright succulent), Se = *Suaeda esteroa*, (short-lived succulent subshrub), Sv = *Salicornia virginica* (perennial succulent subshrub), and Tc = *Triglochin concinna* (winter ephemeral succulent graminoid).

order to evaluate rooting depths with methods comparable to those used in the companion greenhouse experiment (G. Sullivan, unpublished data). Following collection, samples were transported to the laboratory, refrigerated, and carefully rinsed over a 0.45-mm screen. All roots and rhizomes were collected, dried, and weighed. It was not possible to sort root samples by species.

By 2000, a substantial "turf" of green and blue-green algae had accumulated on the marsh surface. This was scraped off the soil surface and rinsed separately from roots.

Shoot sampling

In January 2000, shoots were harvested within a randomly located subplot (20 × 120 cm, encompassing six original plants) within each plot. All aboveground vascular plant material was clipped at the soil surface, sorted by species, and bagged. Any vascular plant litter on the soil surface and plant fragments that could not be identified to species were classified as litter and bagged separately. Plant material was returned to the laboratory, refrigerated, and rinsed over a 0.45-mm screen to remove adhering soil and salt. Tissue samples were collected, dried, and weighed. We classified shoot biomass of each species in a plot as either planted or unplanted based on the original assemblage planted in that plot.

TKN (total Kjeldahl nitrogen) analysis

All soil and tissue samples were analyzed for N concentration. Root samples were analyzed by depth, although samples from some cores in 1999 were com-

posited across depths because of low total biomass. In addition, we analyzed only the N concentration of root samples from 0 to 18 cm depth, because biomass from 18 to 24 cm was too low. Algal turf samples were analyzed for N concentration separately from root samples. Shoots were analyzed separately by species within each plot, and litter samples were also analyzed separately for each plot. Soil samples were ground with a mortar and pestle, and tissue samples were ground with a Wiley mill to pass a number 40 mesh screen (0.42-mm openings). A subsample (0.2 g for soils; 0.4 g for tissue samples) was digested using a standard Kjeldahl digestion, and the nitrogen concentration (TKN) of the digestate was analyzed using an autoanalyzer. The N pool for each plot was calculated based on root, shoot, litter, and turf tissue biomass and tissue N concentrations.

Statistical analysis

We used a two-way ANOVA with interactions (factors: block and species richness) to test for effects of species richness on soil N concentrations, root and shoot biomass, unplanted biomass, turf biomass, tissue N concentrations, and total N accumulation. The 15 plots of 0, 3, and 6 species were used in this analysis, along with 15 randomly chosen 1-species plots. In order to test for species-specific effects on the same parameters identified above, we used a two-way ANOVA without interactions (factors: block and species), with the five replicate plots of each of the eight species planted alone. In all cases, multiple comparisons were made using Tukey's post hoc tests.

In order to evaluate whether the inclusion of the regionally dominant species (Sv) was driving the relationship between species richness and function, we performed regression analyses of species diversity vs. total biomass and N retention in 2000 for all plots and for those without Sv. For this analysis we first used the 15 plots of 0, 3, and 6 species and the 15 randomly chosen 1-species plots (total $n = 60$), and then we repeated the regression for plots without Sv, including 0-species plots ($n = 15$), 1-species plots ($n = 13$), 3-species plots ($n = 8$), and 6-species plots ($n = 3$; total $n = 39$). All data were analyzed using SYSTAT version 9 (SYSTAT 1999). Means ± 1 SE are reported in the text.

RESULTS

Soils

At the time of planting (April 1997), surface (0–5 cm) soil TKN concentrations averaged 0.353 ± 0.008 mg/g, while in August 1999, the mean surface concentration was slightly higher (Table 2). Soil N concentrations in surface samples increased with increasing species richness in August 1999, with 6-species plots being greater than unplanted plots ($P = 0.009$; Table 2). There was no difference among the 1-species

TABLE 2. Mean soil TKN concentrations (mg/g) from August 1999 and August 2000 at the Tidal Linkage, Tijuana Estuary, California.

Treatment	1999		2000	
	0–5 cm	5–15 cm	0–5 cm	5–15 cm
Overall mean ($n = 85$)	0.398 ± 0.010 †	0.230 ± 0.005	0.464 ± 0.013	0.224 ± 0.006
Unplanted ($n = 15$)	0.348 ± 0.024	0.222 ± 0.008	0.371 ± 0.016	0.223 ± 0.011
1-species	0.396 ± 0.020	0.239 ± 0.011	0.451 ± 0.025	0.221 ± 0.013
3-species	0.404 ± 0.029 ‡	0.226 ± 0.014	0.528 ± 0.037	0.231 ± 0.022
6-species	0.469 ± 0.026	0.258 ± 0.010	0.487 ± 0.029	0.234 ± 0.014
Bm ($n = 5$)	0.393 ± 0.024	0.246 ± 0.025	0.477 ± 0.081	0.234 ± 0.027
Fs	0.406 ± 0.029	0.212 ± 0.015	0.452 ± 0.050	0.191 ± 0.019
Jc	0.408 ± 0.036	0.227 ± 0.018	0.453 ± 0.064	0.235 ± 0.028
Lc	0.389 ± 0.031	0.236 ± 0.013	0.437 ± 0.041	0.214 ± 0.020
Sb	0.370 ± 0.036	0.208 ± 0.014	0.484 ± 0.033	0.206 ± 0.032
Se	0.418 ± 0.032	0.234 ± 0.024	0.554 ± 0.051	0.216 ± 0.024
Sv	0.412 ± 0.037	0.236 ± 0.017	0.526 ± 0.029	0.224 ± 0.026
Tc	0.311 ± 0.028	0.201 ± 0.019	0.354 ± 0.042	0.223 ± 0.016

Note: See Table 1 for species names.

† One sample missing data ($n = 84$).

‡ $n = 14$.

plots ($P = 0.361$); i.e., there was no species-specific effect. Soils at lower depths (5–20 cm) had lower N concentrations than surface samples. There was no effect of increasing species richness ($P = 0.067$) or any species-specific effect ($P = 0.458$) in the samples from 5 to 20 cm (Table 2). We found a block effect ($P = 0.017$) for surface soil in April 1997, with the highest concentrations at the east end of the site (block E, mean = 0.386 ± 0.017 mg/g). Differences among blocks also were significant in August 1999 in surface soils ($P = 0.027$) and in deeper soils ($P = 0.008$), although patterns varied with higher values for surface soils in central blocks (B and C) and higher values in block E for samples from 5 to 20 cm.

As in 1999, soil N concentrations increased with increasing species richness in surface samples in August 2000 ($P < 0.001$; Table 2), with both 3- and 6-species plots being greater than unplanted plots. There was no effect of species richness on samples from 5 to 20 cm ($P = 0.841$), and there was no species-specific effect in 2000 in either surface samples ($P = 0.226$) or those from depth ($P = 0.714$). Block effects were significant at both depths (0–5 cm, $P = 0.027$; 5–20 cm, $P < 0.001$); however, trends varied by depth.

Root biomass, 1999 and 2000

In both 1999 and 2000 (two and three years after planting), root biomass (which includes rhizomes) increased with increasing species richness (Fig. 2; $P < 0.001$ for both 1999 and 2000). Plots with 6 species had more root biomass than plots with 1 species in both years ($P = 0.011$ in 1999 and 0.029 in 2000), while 3-species plots were intermediate (Fig. 2). Unplanted plots had less root biomass than planted plots in all cases ($P < 0.01$), except for comparisons between 1-species plots and unplanted plots in 1999 ($P = 0.061$). Root biomass approximately doubled from 1999 to 2000; 3-species plots increased from $175.7 \pm$

30.6 to 440.2 ± 65.8 g/m², while 6-species plots went from 250.2 ± 25.5 to 498.9 ± 63.7 g/m². Despite rapid development, root biomass at the Tidal Linkage remained substantially below values found in natural salt marshes at Tijuana Estuary, which were $\sim 1426.5 \pm 280.8$ g/m² in multiple-species areas ($n = 8$) and 1204.8 ± 182.7 g/m² in monoculture areas ($n = 7$) dominated by Sv (based on cores collected in September 1998 to 25 cm; Pacific Estuarine Research Laboratory, unpublished data).

In 1-species plots, there were species-specific differences in root biomass accumulation in both 1999 ($P < 0.001$) and 2000 ($P < 0.001$). Single-species plots with Sv and Jc accumulated the greatest root biomass (Fig. 2) with values close to 500 g/m² in 2000. Patterns among species were similar in both years, with Sv and Jc also having the greatest root biomass in 1999. Bm, Lc, and Fs had intermediate values of root biomass in both years, followed by Se and Sb. Tc plots had the lowest biomass in both years (Fig. 2). All species had large increases in root biomass between 1999 and 2000 (up to 500% increase for Tc), with most species increasing between 50 and 100%.

In all cases, root biomass was greatest in the top 0–6 cm, with 63%, 67%, and 64% of biomass in the surface sections of 1-, 3-, and 6-species plots, respectively, in 2000. The percentage of roots in the 18–24 cm section ranged from 5.2% to 6.0% across these treatments. Within the 1-species plots, the percentage of root biomass in the surface sections ranged from 54% to 68% for all species, with the exception of Sv (75%) and Lc (45%). Deep roots (in the 18–24 cm section) ranged from 4.0% to 6.0% for all species except Bm (8.2%), Lc (9.2%), and Tc (9.6%).

The biomass of algal turf on the sediment surface was 4–6 times greater in planted plots (52.0 ± 10.4 g/m², 1-species; 51.4 ± 12.6 g/m², 3-species; and 70.3

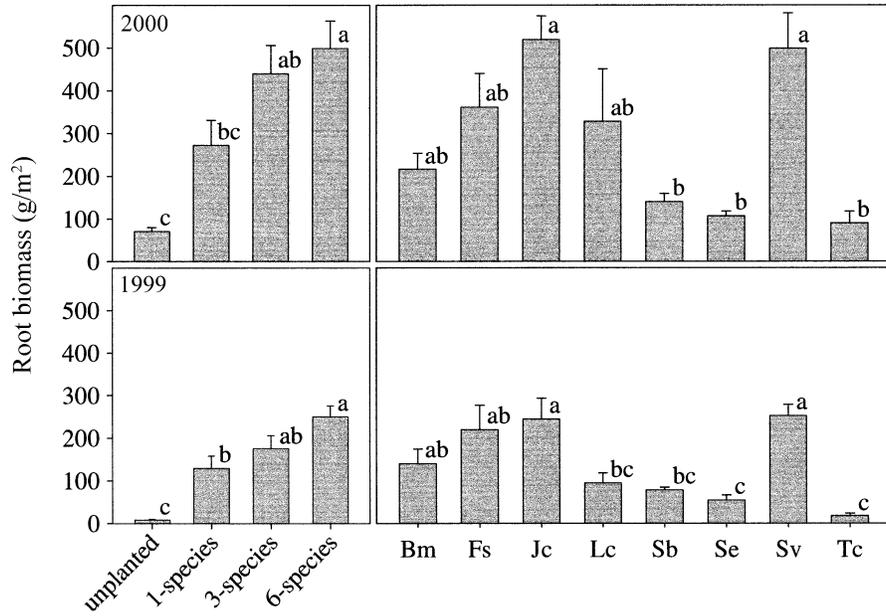


FIG. 2. Mean root biomass in 1999 and 2000 (+1 SE). Means by species-richness treatments are on the left, and means for each of the individual species, planted alone, are on the right. Different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviations are explained in the Fig. 1 legend.

$\pm 12.6 \text{ g/m}^2$, 6-species) than in unplanted plots ($12.1 \pm 2.8 \text{ g/m}^2$; $P < 0.039$). In the 1-species plots, turf biomass ranged from 20.8 ± 6.3 (Tc) to 82.6 ± 20.5 (Fs) g/m^2 , but there were no significant species-specific effects on turf biomass ($P = 0.211$).

Shoots and total biomass, 2000

As with roots, shoot biomass increased with increasing species richness ($P < 0.001$; Fig. 3). Six-species plots averaged $496.7 \pm 65.8 \text{ g/m}^2$ and were greater than

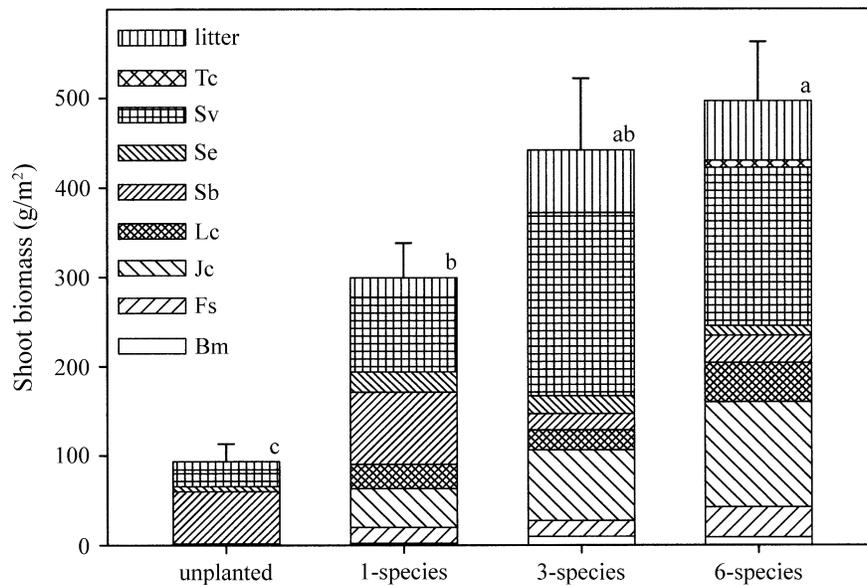


FIG. 3. Mean shoot biomass in 2000 for species-richness treatments (+1 SE). Bars are divided to indicate the amount that individual species contributed within each species-richness treatment. The contribution from litter (undifferentiated by species) is also indicated. Different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviates are explained in the Fig. 1 legend.

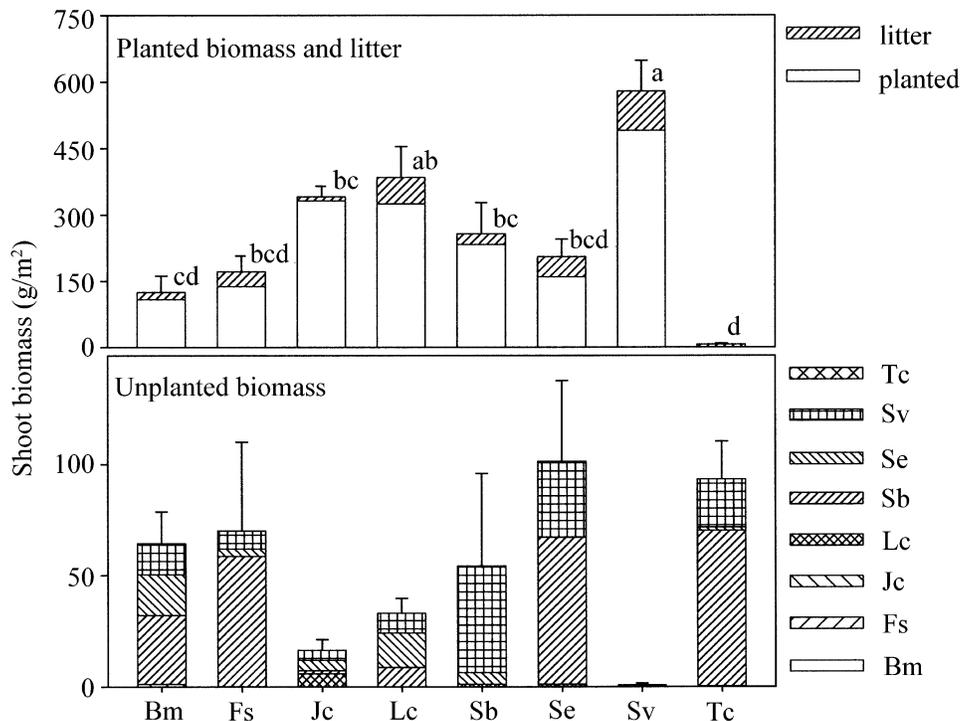


FIG. 4. Mean shoot biomass in 2000 in 1-species plots for planted (top) and unplanted species (bottom). In the top panel, bars are divided to indicate the contribution from the planted species and from litter. In the bottom panel, the bars are divided to indicate the amount that other species contributed as unplanted biomass. Different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviations are explained in the Fig. 1 legend.

1-species plots (299.3 ± 38.7 g/m²; $P = 0.026$), with 3-species plots being intermediate (441.9 ± 79.8 g/m²). Unplanted plots had substantially less biomass than all planted plots (93.5 ± 19.7 g/m²; $P < 0.02$ for all multiple comparisons). After three growing seasons, the average amount of shoot biomass that accumulated in the planted plots was similar to root biomass across all species levels (Figs. 2 and 3). We lack recent data on biomass of multispecies vegetation in Tijuana Estuary; however, Zedler et al. (1980) found that peak biomass (live, dead, and litter) on the marsh plain averaged 915–1150 g/m² over a three-year period. Also, Covin and Zedler (1988) measured 1316 g/m² for Sv in Tijuana Estuary in August, and Boyer et al. (2001) found 444 g/m² in areas dominated by Sv in Mugu Lagoon (240 km northwest of Tijuana Estuary) in January and 999 g/m² at peak biomass in June and August.

Sv and Lc had the greatest shoot biomass in plots where each was grown alone (Fig. 4), with Sv plots averaging 579.6 ± 68.5 g/m² and Lc averaging 385.0 ± 69.8 g/m². Tc shoot biomass was less than all other species, with only 7.0 ± 1.9 g/m², which was comparable to shoot biomass that accumulated in the unplanted plots (9.2 ± 3.0 g/m²). The five other species ranged from 126 to 341 g/m². Sv had the greatest total biomass (1079.9 ± 128.3 g/m²), which was greater than all other species except for Jc and Lc. Tc was lowest

and different from all except Sb and Se. Among individual species, Fs had the greatest root:shoot ratio (1.71), followed by Jc (1.45) and Bm (1.45), with Sb (0.49) and Se (0.38) having the lowest root:shoot ratios. Lc, Sv, and Tc all had root:shoot ratios between 0.86 and 0.91.

The role of individual species was indicated by the relative contribution of each species to the overall shoot biomass in the multispecies plots. As in the 1-species plots, Sv was the dominant species in terms of biomass. Sv contributed 55% and 41% of the shoot biomass in all of the 3- and 6-species plots, respectively (Fig. 3), substantially more than what would be expected if all 8 species contributed equally (12.5%). The only other species that contributed >12.5% in the 6-species plots was Jc (27%). Lc was third with 10%, followed by Sb with 7.1%. All other species contributed 3% or less to the total shoot biomass in the 6-species plots. In the 3-species plots, Jc contributed 21% and all other species contributed 6% or less.

Average root:shoot ratios in the 1-, 3- and 6-species plots were 0.92, 1.24, and 1.11, respectively. The effect of species richness on total biomass (roots + shoots) was significant ($P < 0.001$), with 6-species plots greater than 1-species plots ($P = 0.011$), and 3-species plots being intermediate. Regression analysis confirmed the effect of species richness on total biomass ($r^2 = 0.34$,

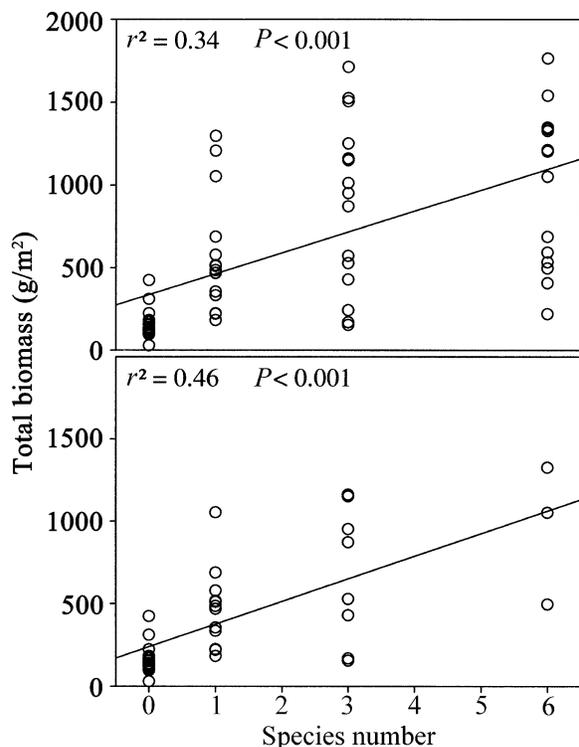


FIG. 5. Relationship between the total biomass (including roots, shoots, and litter, but not turf) and the number of species planted for plots with *Salicornia virginica* (top) and without (bottom); $n = 60$ (15 for all levels of species richness) in the top panel, and $n = 39$ (15 for 0 species, 13 for 1 species, 8 for 3 species, and 3 for 6 species) in the bottom panel.

$P < 0.001$ for all plots; Fig. 5), and indicated that this relationship was even stronger in plots without Sv ($r^2 = 0.46$, $P < 0.001$ for plots without Sv, Fig. 5).

Biomass of unplanted species

A number of unplanted species invaded the experimental plots in year three after being weeded in years one and two. Colonization in the unplanted plots led to an average diversity of 3.1 species at the end of year three, attributable almost entirely to the three most common species: Sb, Sv, and Se. Within the unplanted plots, these three species contributed 97% of the biomass, with Sb contributing 69%, Sv 22%, and Se 7%. Of the other five species, only Fs and Jc were found in unplanted plots.

The biomass in 1-species plots serves as an index of changes in plant diversity due to species' abilities to recruit into other plots and to suppress recruitment by other species (Fig. 4). The most common invading species in the 1-species plots were Sb (54% of the total invader biomass in 1-species plots), Sv (32%), and Se (11%). Lc accounted for 2% of the invader biomass, and all other species accounted for <1%. Sb and Sv also dominated the biomass of unplanted species in the multispecies plots; Sb accounted for 53% of the un-

planted biomass in 3-species plots and 37% in the 6-species plots, while Sv accounted for 42% in 3-species plots and 52% in 6-species plots.

In the 40 1-species plots, the biomass of invaders was suppressed in relation to the biomass produced by the planted species (log transformed, $P < 0.001$, $r^2 = 0.35$). Sv plots had the least biomass from unplanted species, with only 0.1% of the total biomass in the plot coming from species not planted to the plot (Fig. 4). Jc plots had 5% of total biomass from unplanted species, followed by Lc (8%) and Sb (17%). Plots planted with Fs, Se, and Bm all ranged from 29 to 34%. At the other extreme, unplanted species were responsible for 93% of the total biomass in plots where Tc was planted alone.

N concentrations

Average N concentrations for root tissues in the multispecies plots were 12.6 ± 0.4 mg/g (6-species) and 13.6 ± 0.6 mg/g (3-species) (Fig. 6). Root N concentrations in the single-species plots averaged 14.8 ± 1.0 mg/g. Sb had the highest tissue root concentration (19.2 ± 0.4 mg/g), followed by Tc (17.0 ± 0.9 mg/g) and Se (16.5 ± 0.5 mg/g). Se, Bm, Sv, and Fs all ranged from 16.5 to 13.0 mg/g, and Jc averaged 8.3 ± 0.5 mg/g. Turf N concentrations were slightly higher than root concentrations, with the turf from Jc plots being lowest at 11.2 ± 1.2 mg/g and turf from other 1-species plots ranging from 15.6 to 23.3 mg/g (Fig. 6). Litter ranged from 9.7 to 16.1 mg/g in the single-species plots (Fig. 6). There were species-specific effects on shoot N concentrations in the 1-species plots ($P < 0.001$; Fig. 7), with Tc having the greatest concentration and Jc having the lowest. When averaged across all shoot samples from the experiment, tissue concentrations of individual species showed similar patterns, although the range in N concentration was less. Shoot N concentrations for most species ranged from 12 to 17 mg/g (Fig. 7).

N pools

Differences in the N pools among plots reflected differences in biomass rather than differential N concentrations. Roots and shoots each contributed about equally to the N pool in the multiple-species plots (Fig. 8). As with biomass, the majority of the N root pool accumulated in the surface 0–6 cm, with 69% of the total in 6-species plots and 73% in the 3-species plots. The turf N pool was 0.99 ± 0.14 g N/m² in 6-species plots and 0.76 ± 0.16 g N/m² in 3-species plots. For individual species, the turf pool averaged ~14% of the vascular plant pool. The turf N pool was 23% of the vascular plant N pool for Sb (maximum proportion) and 8% for Sv (minimum).

More N accumulated in tissues in 6-species plots than in 1-species plots ($P = 0.03$; Fig. 8). As with biomass results, the 3-species plots were intermediate between these two values. A total of 11.6 g N/m² ac-

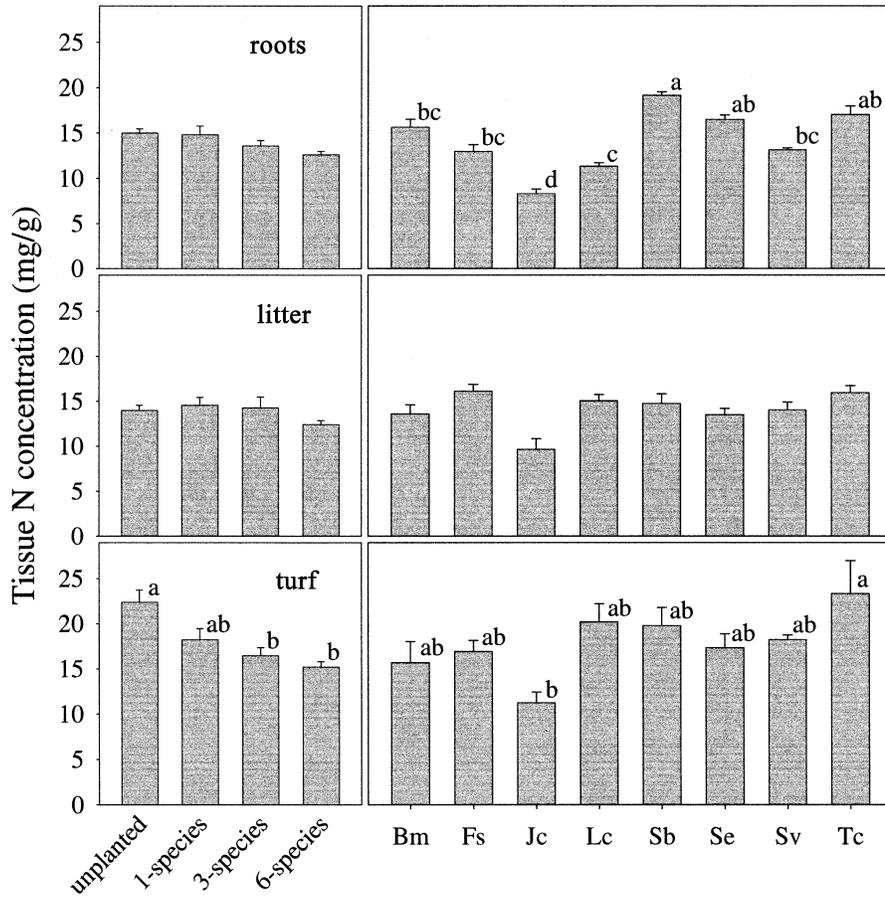


FIG. 6. Mean tissue N concentrations for root (top), litter (middle), and turf (bottom) in 2000 (+1 SE). Means by species-richness treatments are on the left, and means for each of the individual species, planted alone, are on the right. Different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviations are explained in the Fig. 1 legend.

accumulated in plant tissues and litter within the 6-species plots. Regression analysis indicated that the relationship between species richness and N retention was even stronger in plots without Sv ($r^2 = 0.43$, $P <$

0.001 , [total N = $3.38 + 1.37 \times$ species number], $n = 39$) than for all plots in the richness analysis ($r^2 = 0.32$, $P < 0.001$, [total N = $4.48 + 1.40 \times$ species number], $n = 60$).

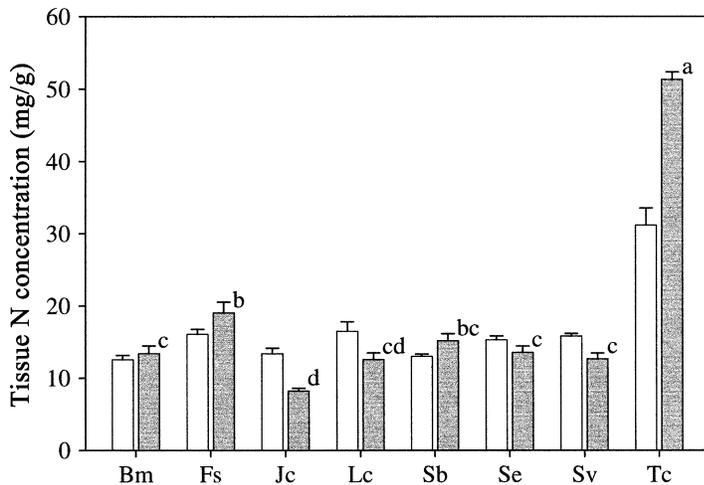


FIG. 7. Mean tissue N concentrations for shoots in 2000 (+1 SE). Open bars indicate means for all samples collected, both planted and unplanted, for a species, and shaded bars indicate means only for samples from plots where a species was planted in 1-species plots. For the data from 1-species plots, different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviations are explained in the Fig. 1 legend.

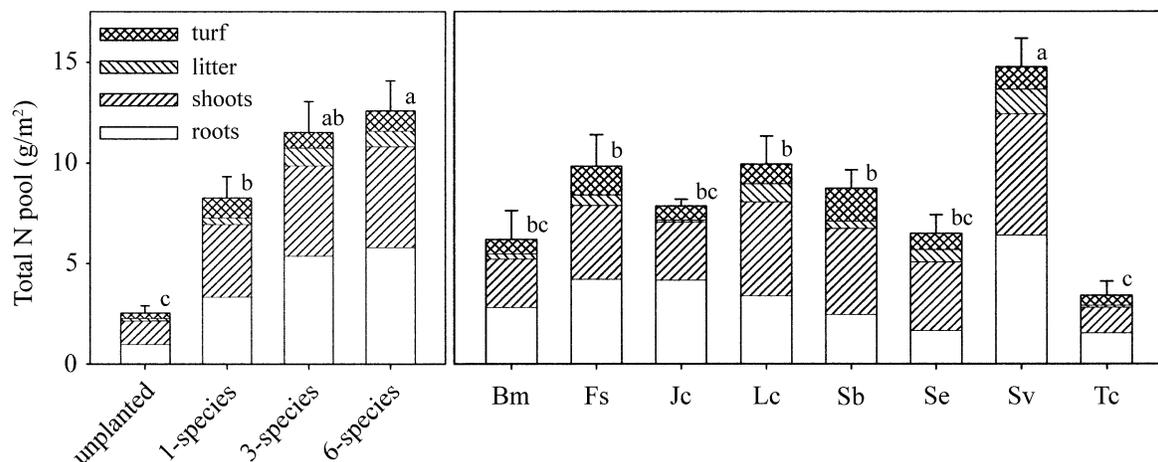


FIG. 8. Mean N accumulation in 2000 (± 1 SE). Means by species-richness treatments are on the left, and means for each of the individual species, planted alone, are on the right. Bars are divided to indicate the amount contributed by roots, shoots, litter, and turf. Different lowercase letters above data bars indicate that means were significantly different ($P > 0.05$) based on Tukey's multiple comparisons. Species abbreviations are explained in the Fig. 1 legend.

In the 1-species plots, the species planted significantly affected the size of the N pools ($P < 0.001$). More N accumulated in Sv plots than in any other 1-species plots, with a total of ~ 13.7 g N/m², not including turf N (Fig. 8). Lc, Fs, Jc, Sb, Se, and Bm had midrange values of N accumulation, with 5.5 to 9.0 g N/m² in their tissues. Tc accumulated only 2.9 g N/m², significantly less than Sv, Lc, and Fs. The contribution of individual species to the shoot N pool in the multispecies plots followed biomass patterns, with Sv contributing 52% and 42% of the N pool in the 3- and 6-species plots, respectively (compared to 12.5% if all eight species contributed equally). Jc contributed 22% in the 3-species plots and 27% in the 6-species plots. All other species contributed 9% or less to the shoot N pool.

DISCUSSION

The southern California salt marsh is a useful model for testing the relationship between diversity and ecosystem functions, because the number of native species is small, and the species commonly co-occur in assemblages of two to six species, as Vitousek and Hooper (1993) recommend for such experiments. Most studies that have evaluated the effects of species number have occurred in species-rich grassland ecosystems, with up to 32 species in the diversity treatments (Tilman et al. 1997, Hector et al. 1999). Our experimental treatments represent actual diversity levels at the 2×2 -m scale, with a range from 6 species/4 m² in relatively undisturbed wetlands to a single species in areas with hydrologic modifications (Zedler et al. 2001). While most diversity experiments have addressed only biomass accumulation, we added N retention, a key concern for salt marsh restoration and functioning. Hence our results inform both basic ecological understanding and restoration and management. The need to understand

the implications of biodiversity for the restoration and management of ecosystems is critical (MacMahon and Holl 2001, Tilman et al. 2001), and because a suitable goal of restoration is to provide functional ecosystems (Ehrenfeld and Toth 1997), it is prudent that ecologists test theory and develop tools for using diversity to provide maximally functioning ecosystems (MacMahon and Holl 2001).

Differences among species

In our field experiment, we found unique features of plots planted with one species. Sv was dominant in many aspects. Within the 1-species plots, Sv ranked first in all measures of biomass and N retention, except for belowground biomass in 2000, where it ranked second. Sv also dominated in the multispecies plots. In the 3-species plots where it was planted (7 of 15 plots), Sv contributed 82.5% of the shoot biomass instead of the 33.3% expected if all 3 species contributed equally. In the 6-species plots where it was planted (12 of 15 plots), Sv contributed 53.5% of shoot biomass instead of 16.7%, assuming equal contribution from all species. This level of dominance helps explain why Sv is the most abundant species in southern California salt marshes.

Jc was the only other species that consistently contributed substantial biomass to multispecies plots, both as roots and shoots. Tc had the highest N concentration in shoots, similar to greenhouse results (Sullivan and Zedler 1999), while Sb had the highest N concentration in roots. G. Sullivan (*unpublished data*) found more individuality among the same species in a greenhouse experiment, with each of the eight species excelling in at least one attribute. Other species also made contributions in the field in terms of canopy complexity, with each species having unique canopy characteristics (Keer and Zedler 2002). Species effects on canopy

characteristics were also more obvious in the greenhouse than in the field experiment (Keer and Zedler 2002). Note that in the field, plots were allowed to change composition in year three, but greenhouse plots had constant composition over the two-year experiment.

Our plots changed in part due to recruitment, but they were also affected by differences in individual species' ability to suppress recruitment. Earlier diversity experiments maintained original planting treatments by weeding over extended periods (e.g., Tilman et al. 1997) and do not provide direct insight into the temporal dynamics of species diversity. Suppression of voluntary recruits (unplanted species) varied by species, and the species that developed substantial biomass in the 1-species plots (e.g., Sv and Jc) had the greatest effect in suppressing recruitment of other species, confirming the link between cover or biomass, available resources, and invasibility (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Symstad 2000). The ranking of shoot biomass of species planted to 1-species plots (Sv > Jc, Lc, Sb, Se, Fs, Bm, Tc) was almost the same as their ranking for suppression of recruitment (Sv > Jc, Lc, Sb, Bm, Fs, Tc, Se). Multiple-species plots with Sv had lower diversity in the 20 × 120 cm subplot that was sampled for aboveground biomass (3.1 and 5.2 species for 3- and 6-species plots) than in plots where Sv was absent (4.5 and 7.3 species for 3- and 6-species plots; $P = 0.048$ for 3-species plots and 0.024 for 6-species plots, pooled variance t test), confirming the ability of Sv to suppress establishment of other species.

At Tijuana Estuary, the regionally dominant species contributed the greatest biomass to experimentally planted plots, retained the most N, established frequently from seed, and reduced recruitment by other species. If our results hold at increasing scales of restoration, we would expect unplanted salt marshes to be limited to a few easily establishing species and to develop ecosystem functions more slowly than sites planted with multiple species. If particular species are not planted initially, their contribution to the ecosystem may be severely limited, and unplanted sites might never achieve the functional levels of species-rich sites.

Species-richness effects

Our results indicate that even in an ecosystem with relatively low plant diversity, species richness can be important in determining biomass and N retention. We found a consistent increase in ecosystem functioning with increased species richness, and similar responses in biomass and N retention both above- and belowground. Diversity levels predicted 34% of the variability in total biomass and 32% of the variability in total N retention. After three years, 6-species plots had 411% more N in biomass than unplanted plots and 59% more N than the average 1-species plots, although the 1-species Sv plots were comparable to the multispecies plots. In a fresh water aquatic plant community with

four species, Engelhardt and Ritchie (2001) recently showed that increased vascular plant diversity resulted in greater total plant (vascular and algal) biomass and P retention, but variability was high, and their r^2 value for the number of species and total biomass (including algae) was only 0.04 with $P = 0.06$. Although we explained much more of the variance, it is understandable that the use of 15 unique assemblages within the 3- and 6-species treatments still had unexplained variability. Under controlled conditions in a greenhouse, G. Sullivan (*unpublished data*) replicated each assemblage and confirmed our findings from the field, with even greater statistical significance for species diversity treatments.

Richness vs. species-specific effects

Debate over how to interpret results from diversity experiments has focused on the effect of species number on ecosystem functioning vs. the effect of species composition, i.e., the chance inclusion of a particular species (called a sampling effect [Huston 1997, Tilman et al. 1997]). Because both species number and composition have been shown to play significant roles in ecosystem functioning (e.g., Hooper and Vitousek 1997, Tilman et al. 1997, 2001, Engelhardt and Ritchie 2001), there is now a need for unifying theory on the relative importance of these two factors across different systems. Given that Sv dominates most southern California salt marshes and that biomass and N accumulation rates for Sv grown alone were similar to the multispecies plots, this ecosystem might be expected to show a strong sampling effect as the driver for species-richness effects. However, analysis of biomass and N retention data in plots where Sv was not planted also showed a significant effect of species number (Fig. 5), indicating that Sv is not the only species responsible for increased function.

Two mechanisms by which species-rich vegetation could increase biomass and N retention in plots of higher diversity are the differential use of the canopy in absorbing light and the differential use of the root zone in obtaining N. The former is supported by the findings of Keer and Zedler (2002) in this same experiment, namely, that species-rich plots had more canopy layers than species-poor plots. In Switzerland, Spehn et al. (2000) found increases in average height and other canopy characteristics with increasing species richness; they favored complementary use of light as the best explanation. We agree that complementary canopies and increased layering of leaves contribute to the richness effect.

Evidence for spatial differentiation belowground is weak in our results. We did not find large differences in rooting depths or distributions among species, although our 6-cm sampling strata might not be optimal for identifying differences. Alternatively, there could be temporal sharing of belowground resources. This is likely for some species, since we know that active pe-

riods of growth differ substantially. Tc grows vigorously in winter and reaches peak biomass by late spring, while Sb seedlings appear around this time period and achieve maximum biomass in late summer (Zedler et al. 2001). Even the evergreen perennials tend to be most active throughout late spring and summer (Onuf 1987); their temporal patterns of N loss (and availability for uptake by associated species) might explain why only a small subset of the possible combinations of the marsh plain's eight halophyte species actually occur in the region's salt marshes (H. N. Morzaria-Luna, J. B. Zedler, J. C. Callaway, and G. Sullivan, *unpublished manuscript*), and temporal segregation of resource use could account for some of the species-richness effect. Complementary use of N by Tc and Sb is being explored using ^{15}N (H. N. Morzaria-Luna, *personal communication*), and more work of this kind is needed.

Applications to wetland restoration

Our diversity-function experiment is the first to focus on the relationship of species diversity and the development of ecosystem functions in a restoration setting. The marsh plain was initially bare, and we maintained planted assemblages and unplanted plots for two years; this kept the assemblages constant in the planted plots and allowed us to compare recruitment potential in the unplanted plots over two growing seasons. While this served our scientific goals, the removal of seedlings slowed restoration. In year three, we allowed all plots to accumulate new species through seedling recruitment, and our subsequent evaluation of changes in species diversity indicated the likelihood that a plot would increase in species richness over time. The value of planting for restoration projects has been debated, but clearly planting is important for some restoration attempts (e.g., see Mitsch et al. 1998, Streever and Zedler 2000). Planting is especially common for small, isolated wetlands and for projects where particular species of interest may be dispersal limited. In arid-region wetlands, lack of planting risks high rates of evapotranspiration at the soil surface, leading to salt crust formation and lower plant survival (Zedler et al. 2003).

Performance of unplanted plots.—Our inclusion of bare plots is relevant to restoration projects that do not involve planting, instead allowing the plant community to develop the diversity and function of natural, reference ecosystems on its own (Mitsch et al. 1998). Our data indicate that in the short term, unplanted plots are not likely to support high levels of diversity or function, in large part because only three of the eight species are likely to recruit seedlings (Lindig-Cisneros 2001). Sv, Sb, and Se established in the first year following weeding, but diversity is unlikely to increase over time; rather, we expect Sb and Se to be overwhelmed by the regional dominant (Sv) in the unplanted plots. In our multispecies plots that contained Sv and other species, Sv consistently became the dominant. For example, in

the 3-species plots that were planted with both Se and Sv ($n = 3$), Sv averaged 87% of the shoot biomass in year three, and in the 3-species plot with Sb and Sv ($n = 1$), Sv comprised 88% of the shoot biomass. Se and Sb were either absent or contributed minimal biomass to these plots. Because Sb and Se are an annual and a short-lived perennial species, respectively, they may not remain where environmental conditions favor perennial vegetation, i.e., the more well-drained sites (Ferren et al. 1997). Also, in our experimental plots, Sv was able to suppress recruitment of other species. This pattern of Sv dominance seems to be most likely where tidal flushing is impaired and soils become dry and hypersaline. At Los Peñasquitos Lagoon, which has undergone long periods without tidal wetting, Sv formed a monotype that accumulated 2.5 times the biomass of the more diverse vegetation of Tijuana Estuary (Zedler et al. 1980). Based on this evidence, we expect Sv to continue to contribute the majority of biomass in unplanted plots of this relatively well-drained marsh plain.

Large-scale salt marsh restoration projects in California are even more likely to be dominated by Sv, unless other species are introduced. Unlike our experiment, in which we introduced all eight species in relatively even numbers, and for which most reproduced by seed, the typical restoration site would likely receive seeds primarily from Sv, the most common salt marsh plant in the region (Zedler 1982, Sullivan 2001, Zedler et al. 2001). Sv's combined ability to (a) gain access to a restoration site, (b) recruit into open patches and (c) dominate salt marsh biomass suggests that other species need to be planted. We suggest that species pools for other regions and ecosystem types be evaluated similarly. Species with superiority in dispersal, recruitment, and biomass accumulation should colonize restoration sites unaided; others could be targeted for planting, especially where the objective is the establishment of diverse assemblages. If species that rank low in seed availability and recruitment are not planted initially, they might not establish on their own or their relative contribution to the ecosystem might be very small. Among the most common shortcomings of restored wetlands is their low species richness relative to reference sites (NRC 2001). Unless pains are taken to introduce species with low dispersal, recruitment, and growth rates, the opportunity to achieve positive effects of species-rich vegetation could be lost.

Performance of multispecies plots.—Given the significant effects of species richness on biomass and N retention, we recommend using a diversity of species in future plantings and experiments. For salt marsh restoration efforts, the link between diversity and N retention has the most important management implications because many restoration projects are located in areas with coarse soil and low N conditions (Lindau and Hossner 1981, Craft et al. 1988, 1991, Langis et al. 1991). Restoration techniques that improve N re-

tention, such as the planting of diverse assemblages, can be used to accelerate the overall development of a restored wetland.

The link between diversity and function in our salt marshes also has implications for the management of degraded ecosystems. Many coastal salt marshes in southern California have altered hydrology, and these marshes tend to have lowered plant species richness (Zedler 2001, Zedler et al. 2001). There is concern for the overall biodiversity of wetland species in the region because hydrological modifications are increasingly common. In addition to direct impacts from hydrological modifications, our data indicate that modified sites could have reduced ecosystem functioning due to biodiversity declines. If regional diversity declines are enough to reduce propagule availability, this could further affect local diversity (Levine 2000). Loreau et al. (2001) indicate that regional diversity effects and dispersal limitations are likely to feed back and reduce the pool of colonizers. These links provide further support for the need to manage the region's remaining wetland habitats to enhance and sustain biodiversity.

We conclude that the planting of multiple species significantly increased average rates of both biomass and N accumulation. The effect of species richness was not due solely to the chance inclusion of the dominant species (a species-specific effect). Thus, manipulating both species richness and species composition can be an important tool in restoring ecosystem functions. In future restoration projects, we suggest planting multiple species, excluding those that should recruit without assistance.

ACKNOWLEDGMENTS

Our research was supported by funding from the National Science Foundation (DEB 96-19875) and the Earth Island Institute. The Tidal Linkage restoration project was funded by the U.S. Fish and Wildlife Service and the California State Coastal Conservancy with the multiple goals of creating habitat, improving restoration methods, and providing a high-profile educational opportunity. We thank them and the Tijuana River National Estuarine Research Reserve for their support. The research was initiated when all three authors were at the Pacific Estuarine Research Laboratory (PERL) at San Diego State University; we thank all of the students and staff at PERL and the University of Wisconsin who were invaluable in completing the research, including Georgeann Keer, Roberto Lindig-Cisneros, Julie Desmond, Janelle West, and Vicki Tripolitis. Thanks to Lisa Thurn at SDSU for analyzing many TKN samples. We thank two anonymous reviewers who provided helpful comments that improved the manuscript.

LITERATURE CITED

- Bishel-Machung, L., R. P. Brooks, S. S. Yates, and K. L. Hoover. 1996. Soil properties of reference wetlands and wetland creation projects in Pennsylvania. *Wetlands* **16**:532-541.
- Boyer, K. E., P. Fong, R. R. Vance, and R. F. Ambrose. 2001. *Salicornia virginica* in a Southern California salt marsh: seasonal patterns and a nutrient-enrichment experiment. *Wetlands* **21**:315-326.
- 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.
- Buresh, R. J., R. D. DeLaune, and W. H. Patrick, Jr. 1980. Nitrogen and phosphorus distribution and utilization by *Spartina alterniflora* in a Louisiana Gulf Coast marsh. *Estuaries* **3**:111-121.
- Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* **127**:48-58.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylaor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- Covin, J. D., and J. B. Zedler. 1988. Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, California. *Wetlands* **8**:51-65.
- 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., 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.
- Craft, C. B., E. D. Seneca, and S. W. Broome. 1991. Pore-water chemistry of natural and created marsh soils. *Journal of Experimental Marine Biology and Ecology* **152**:187-200.
- Crews, T. E., L. M. Kurina, and P. M. Vitousek. 2001. Organic matter and nitrogen accumulation and nitrogen fixation during early ecosystem development in Hawaii. *Biogeochemistry* **52**:259-279.
- Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* **43**:427-448.
- Daily, G. C. 1995. Restoring value to the world's degraded lands. *Science* **269**:350-354.
- Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515-522.
- Ehrenfeld, J. G., and L. A. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restoration Ecology* **5**:307-317.
- Engelhardt, K. A. M., and M. E. Ritchie. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature* **411**:687-689.
- Ferren, W. R., H. M. Page, and P. Saley. 1997. Management plan for Carpinteria Salt Marsh Reserve: a southern California estuary. University of California Natural Reserve System and the Museum of Systematics and Ecology, Department of Biological Sciences, University of California, Santa Barbara, California, USA.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405**:220-227.
- Gibson, K. D., J. B. Zedler, and R. Langis. 1994. Limited response of cordgrass (*Spartina foliosa*) to soil amendments in a constructed marsh. *Ecological Applications* **4**:757-767.
- 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.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**:1123-1127.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302-1305.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449-460.

- Jenny, H. 1941. Factors of soil formation: a system of quantitative pedology. McGraw-Hill, New York, New York, USA.
- Keer, G. H., and J. B. Zedler. 2002. Salt marsh canopy architecture differs with the number and composition of species. *Ecological Applications* **12**:456–473.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286–293.
- Langis, R., M. Zalejko, and J. B. Zedler. 1991. Nitrogen assessment in a constructed and a natural salt marsh of San Diego Bay. *Ecological Applications* **1**:40–51.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Lindau, C. W., and L. R. Hossner. 1981. Substrate characterization of an experimental marsh and three natural marshes. *Soil Science Society of America Journal* **45**:1171–1176.
- Lindig-Cisneros, R. A. 2001. Interactions among species richness, canopy structure, and seedling recruitment. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Lindig-Cisneros, R. A., and J. B. Zedler. 2002. Halophyte recruitment in a salt marsh restoration site. *Estuaries* **25**:1174–1183.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grimes, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- MacMahon, J. A., and K. D. Holl. 2001. Ecological restoration: a key to conservation biology's future. Pages 245–269 in M. E. Soulé and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington, D.C., USA.
- Mitsch, W. J., X. Y. Wu, R. W. Nairn, P. E. Weihe, N. M. Wang, R. Deal, and C. E. Boucher. 1998. Creating and restoring wetlands: a whole-ecosystem experiment in self-design. *BioScience* **48**:1019–1030.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97–108.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- NRC (National Research Council. Committee on Mitigating Wetland Losses). 2001. *Compensating for wetland losses under the Clean Water Act*. National Academy Press, Washington, D.C., USA.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–270.
- Onuf, C. P. 1987. The ecology of Mugu Lagoon, California: an estuarine profile. U.S. Fish and Wildlife Service Biology Report 85(7.15). U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Patrick, W. H., Jr., and R. D. DeLaune. 1976. Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuarine and Coastal Marine Science* **4**:59–64.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* **269**:347–350.
- Schlesinger, W. H., L. A. Bruijnzeel, M. B. Bush, E. M. Klein, K. A. Mace, J. A. Raikes, and R. J. Whittaker. 1998. The biogeochemistry of phosphorus after the first century of soil development on Rakata Island, Krakatau, Indonesia. *Biogeochemistry* **40**:37–55.
- Schulze, E.-D., and H. A. Mooney. 1993. *Biodiversity and ecosystem function*. Springer-Verlag, New York, New York, USA.
- Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**:297–305.
- Shaffer, P. W., and T. L. Ernst. 1999. Distribution of soil organic matter in freshwater emergent/open water wetlands in the Portland, Oregon metropolitan area. *Wetlands* **19**:505–516.
- Simenstad, C. A., and R. M. Thom. 1996. Functional equivalency trajectories of the restored Gog-Le-Hi-Te estuarine wetland. *Ecological Applications* **6**:38–56.
- Spehn, E. M., J. Joshi, B. Schmid, M. Diemer, and C. Korner. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* **14**:326–337.
- Streever, W., and J. B. Zedler. 2000. To plant or not to plant? *BioScience* **50**:188–189.
- Sullivan, G. 2001. Establishing vegetation in restored and created coastal wetlands. Pages 119–155 in J. B. Zedler, editor. *Handbook for restoring tidal wetlands*. CRC Press, Boca Raton, Florida, USA.
- Sullivan, G., and J. B. Zedler. 1999. Functional redundancy among tidal marsh halophytes: a test. *Oikos* **84**:246–260.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* **81**:99–109.
- SYSTAT. 1999. SYSTAT 9.0. SYSTAT Software, Richmond, California, USA.
- Tilman, D. 2000. Causes, consequences and ethics of biodiversity. *Nature* **405**:208–211.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* **294**:843–845.
- Valiela, I., and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation. Pages 547–563 in R. J. Reimold and W. H. Green, editors. *Ecology of halophytes*. Academic Press, New York, New York, USA.
- Vitousek, P. M., and D. U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In E.-D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, New York, New York, USA.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, and P. A. Matson. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* **23**:197–215.
- Zedler, J. B. 1982. The ecology of southern California coastal salt marshes: a community profile. United States Department of the Interior, Washington, D.C., USA.
- Zedler, J. B., editor. 2001. *Handbook for restoring tidal wetlands*. CRC Press, Boca Raton, Florida, USA.
- Zedler, J. B., and J. C. Callaway. 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology* **7**:69–73.
- Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *BioScience* **51**:1005–1017.
- Zedler, J. B., H. N. Morzaria-Luna, and K. M. Ward. 2003. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant and Soil* **253**:259–273.
- Zedler, J. B., T. Winfield, and P. Williams. 1980. Salt marsh productivity with natural and altered tidal circulation. *Oecologia* **44**:236–240.