

Aboveground and Belowground Productivity of *Spartina alterniflora* (Smooth Cordgrass) in Natural and Created Louisiana Salt Marshes

KEITH R. EDWARDS* and KAILI P. MILLS

Louisiana Environmental Research Center, McNeese State University, Lake Charles, Louisiana 70609

ABSTRACT: In Louisiana, salt marshes are being created in an effort to offset the large loss of such habitat that has occurred over the last 50 yr. Primary productivity is an important function and indicator of success for salt marsh creation and restoration projects. The aim of this study was to determine whether the aboveground and belowground productivity of the dominant salt marsh grass *Spartina alterniflora* in created marshes in southwest Louisiana began to approximate productivity levels in natural marshes over time. Net annual aboveground primary productivity (NAPP) was measured by a harvest technique, while the ingrowth core method was used to estimate net annual belowground primary productivity (NBPP). NAPP levels were similar to those found in other Louisiana salt marshes, while NBPP levels were similar to or higher than the reported range for *S. alterniflora* studied along the Atlantic and Gulf of Mexico coasts. NAPP tended to decrease as the created marshes aged, but the levels in the oldest, 19 year old, created marsh were still well above values measured in the natural marshes. It was estimated that it would take 35 yr after marsh creation for NAPP in the created marshes to become equivalent to that in natural marshes. NBPP in the created marshes became equivalent to levels found in the natural marshes after 6–8 yr, but then belowground production increased with marsh age, reaching an asymptote that surpassed natural marsh levels. Equivalency in primary productivity has not been reached in these marshes. Elevation also affected productivity, as higher elevational sites with greater topographic heterogeneity had significantly lower aboveground and belowground biomass levels than those with elevations closer to mean sea level. This underscores the need to construct marshes so that their mean elevation and degree of topographic heterogeneity are similar to natural marshes.

Introduction

Coastal wetlands in Louisiana have been, and are continuing to be, lost at a high rate. As a result of both natural and human factors, 3,460 km² of Louisiana coastal wetlands have converted to open water since 1956 (Chabreck 1994; Turner 1997; Day et al. 2001; Gosselink 2001). This loss accounted for 80% of coastal wetland losses in the coterminous United States during this period (Boesch et al. 1994; Chabreck 1994; Bourne 2000). Local governments, the state of Louisiana, and the U.S. government have developed programs to prevent further losses of these coastal wetlands and restore some of the lost habitats. Programs such as Coast 2050 and the Coastal Wetlands Planning, Protection and Restoration Act (CWPPRA, also known as the Breaux Act) provide money (e.g., \$40 million per year from CWPPRA) for wetland restoration projects in Louisiana alone (Raynie et al. 2000).

The use of dredged material has become an increasingly important tool for wetland creation and restoration along the northern Gulf of Mexico coast. The creation of replacement wetlands is considered to be a beneficial use of dredged material (Craft et al. 1988; Landin et al. 1989; Streever 2000). The dredged material is either planted with the desired species (Broome et al. 1988; Craft et al. 1988, 1999; Streever 2000) or constructed to allow natural colonization (Chabreck 1989, 1994; Streever 2000). Natural colonization of dredged sediments is the method used in most salt marsh creation projects along the Louisiana coast (Chabreck 1989; Proffitt and Young 1999).

Trajectories of ecological functions have been used by some researchers to determine the success of marsh creation projects (Simenstad and Thom 1996; Zedler and Callaway 1999, 2000; Morgan and Short 2002; Edwards and Proffitt 2003). The main assumption behind the use of the trajectories is that, as the created marshes age, the ecological functions in them should approximate those in natural reference marshes. In this approach, several functions should be chosen that would best indicate success (Short et al. 2000). One of these

* Corresponding author; current address: Department of Ecology, Faculty of Biological Sciences, University of South Bohemia Branišovská 31, CZ-37005 České Budějovice, Czech Republic; tele: 420/38-777-2259; fax: 420/38-777-2368; e-mail: kredwards59@yahoo.com

important ecological functions is primary productivity.

We compare the aboveground and belowground primary productivity of *Spartina alterniflora* Loisel between natural and created salt marshes in southwest Louisiana. *S. alterniflora* is the dominant plant of tidal coastal salt marshes along the Atlantic and northern Gulf of Mexico coasts of the U.S. and is very important to the trophic structure and ecological functioning of estuaries (Morris and Haskin 1990; Hwang and Morris 1992; Mitsch and Gosselink 2000; Proffitt et al. 2003). It can comprise up to 98% of the plant cover in our study marshes (Edwards and Proffitt 2003). This work was part of a long-term continuing study comparing created marshes, formed with dredged material, to natural salt marshes. Other published work from this study include comparisons of the structural characteristics of the created and natural marshes (Proffitt and Young 1999; Edwards and Proffitt 2003), description of the genetic structure and diversity of *S. alterniflora* (Travis et al. 2002; Proffitt et al. 2003), and the effect of facilitation by *S. alterniflora* on species diversity and succession within the study marshes (Egerová et al. 2003).

There are numerous studies of *S. alterniflora* productivity but only a few compare productivity between natural and created salt marshes (e.g., Webb and Newling 1985; Craft et al. 1999). No such comparative studies have been done in Louisiana. Our objective was to determine whether, over time, net aboveground and belowground annual primary productivity and biomass levels in the created marshes became similar to levels in the natural marshes.

Material and Methods

STUDY SITES

The study sites were located in the Hog Island area of the Sabine National Wildlife Refuge (NWR) in southwest Louisiana (Fig. 1). The Hog Island area is bordered on the east by Calcasieu Lake and the Calcasieu ship channel and to the west by Louisiana Highway 27. It is 8 km south of the town of Hackberry (30°N, 92°20'W). The sediments in this area, and in all of southwest Louisiana (the Chenier Plain), are reworked river deposits that were carried by longshore transport westward from the Mississippi delta. These have a higher clay content than the more sandy direct river deposits in the deltaic plain of southeast Louisiana (Chabreck 1989, 1994; Edwards and Proffitt 2003). Plant species diversity is usually low in these marshes, with the low elevation zones being dominated by *S. alterniflora*, and *Spartina patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene dominating

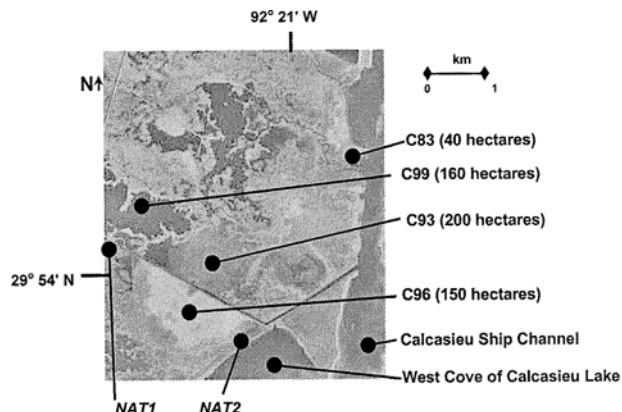


Fig. 1. Location of the study sites in the Hog Island Gully area of the Sabine National Wildlife Refuge (NWR), southwest Louisiana.

in the higher marsh zones (Bertness 1991; Proffitt et al. 2003).

Four marshes were created in the Sabine NWR in 1983, 1993, 1996, and 1999 (referred to as C83, C93, C96, and C99, respectively) using material from regular maintenance dredging activities on the Calcasieu ship channel. The sites chosen for these new marshes were open water areas that had been previously vegetated salt marsh. Marsh creation was done not only to reestablish habitat, but also to reduce erosion of still-existing natural marshes bordering the ship channel (Craft et al. 1999; Proffitt and Young 1999; Penland 2001).

The new marshes were constructed by building containment dikes around the perimeter of sites to contain the dredge slurry. A discharge pipe was placed at various locations in the interior of each site and the dedicated dredge material pumped as a slurry into these areas and allowed to spread, covering the entire site. The dredge slurry was pumped to maximum heights of between 100 and 130 cm National Geodetic Vertical Datum (NGVD), with later dewatering and subsidence expected to result in final elevations similar to those found in nearby natural salt marshes (Penland 2001).

Elevations in the four created and nearby natural marshes were measured using a closed-loop, traverse survey with a Spectrapysics 750 laser level in summer 2000 and referenced to the NGVD. The constructed sites were relatively flat with mean site elevations ranging from about 40 to almost 80 cm NGVD. Mean elevation of the natural sites ranged from 32 to 65 cm NGVD (Table 1). The eastern ends of the C93 and C96 marshes were higher and had greater topographic heterogeneity (measured as elevation range) than the other created sites. These topographic highs were probably associated

TABLE 1. Characteristic features of the created and natural salt marshes sites in the Hog Island area of the Sabine National Wildlife Refuge, southwest Louisiana. Elevations are means \pm 1 SD, with elevation range in parentheses.

Sites	Created/Natural	Age (yr)	Elevation (cm NGVD)	Size (ha)
C83	Created (in 1983)	19	39.27 \pm 5.44 (19.81)	40
C93E	Created (in 1993)	9	64.12 \pm 7.84 (50.90)	~200
C93W	Created (in 1993)	9	57.70 \pm 5.78 (17.68)	
C96E	Created (in 1996)	6	76.54 \pm 11.79 (42.06)	~150
C96W	Created (in 1996)	6	48.44 \pm 3.09 (7.62)	
C99	Created (in 1999)	3	43.42 \pm 6.83 (19.05)	~160
NAT1	Natural	>50	32.65 \pm 5.69 (17.37)	15
NAT2	Natural	>50	65.56 \pm 3.20 (8.84)	40

with placement of the discharge pipe during marsh creation (Proffitt and Young 1999). All of the sites fell within the reported elevational range of *S. alterniflora* (Ellison et al. 1986).

Vegetation was allowed to colonize naturally into the created marshes, either from vegetation rafts floating into the marshes, vegetative expansion, or seed from adjacent natural marshes; this is the common practice with coastal marsh restoration and creation projects in Louisiana (Chabreck 1989; Proffitt and Young 1999). *S. alterniflora* became the dominant plant species in all of the marshes. The exception was the higher elevation eastern end of the C96 marsh, which, although originally dominated by *S. alterniflora* and the opportunistic *Salicornia bigelovii* Torr., eventually became dominated by high marsh and shrub species (Edwards and Proffitt 2003).

The creation of marshes in different years, but with the same source material, produced a chronosequence of sites, which allowed for a "space for time substitution" analysis (Morgan and Short 2002, p. 462). Due to the general dominance of *S. alterniflora* in most locations, the productivity study was limited to this species.

Aboveground and belowground productivity were sampled in 7 sites in the 4 created marshes and in 2 natural marshes (referred to as NAT1 and NAT2), for a total of 9 study sites. All sampling sites were located in the interior portion of each marsh. Marsh descriptions are given in Proffitt and Young (1999), Proffitt et al. (2003), and Edwards and Proffitt (2003). The age and size of each created marsh are given in Table 1. The C93 and C96 created marshes were divided into eastern and western halves (C93E, C93W, C96E, and C96W) based on the observed differences in elevation and vegetation structure in these marshes. The C83 marsh was sampled in two different zones, labeled C83-60 m and C83-green. The C83 marsh suffered from a dieback event that affected Louisiana coastal marshes in 2000 (Stewart et al. 2001), and resulted in the death of at least the aboveground portions of *S. alterniflora* over large areas. In the C83 site, the 60-m zone (being 60 m in from the southern

edge of the marsh, see Edwards et al. 2001) was the part of the marsh most affected by the dieback event, while the green zone was visually unaffected.

ABOVEGROUND PRIMARY PRODUCTIVITY

Sampling for aboveground primary productivity of *S. alterniflora* occurred from June 2001 to September 2002, except for the C99 site, in which sampling continued through December 2002 due to difficulties in collecting samples earlier in the study period. No sampling occurred in October and November 2001 because of mechanical problems. Measurements of aboveground primary productivity closely followed the harvest methods of Shew et al. (1981) and Kaswadji et al. (1990). The method used for study plot selection depended on the growth form of *S. alterniflora* in a particular marsh. *S. alterniflora* grew as large, homogeneous (by visual inspection) stands in the two natural and oldest created marshes (C83 and C93), while only isolated clones were found in the C96W, C96E, and C99 sites. These isolated clones covered from 30% to 50% of the total area in these younger marshes at the time of the study. In sites with large homogeneous stands (NAT1, NAT2, C83-60 m, C83-Green, C93E, C93W), a grid with meter-wide transects was laid within each of the *S. alterniflora* stands. Adjacent transects were separated by 1.0-m wide buffer strips. One transect was chosen at random for each sampling period with 4–6 quadrats (1.0 m² each) selected randomly along the chosen transect for the actual productivity sampling. Each quadrat was divided into four plots, measuring 0.0625 m² (25 \times 25 cm) and located in each corner of the quadrat, with a 50 cm buffer between each plot.

It was not possible to establish sampling grids in the younger created marshes (C96E, C96W, C99), so 4–6 clones were selected haphazardly in each of these sites for each sampling period. Sample plots (0.0625 m²) were placed linearly in the outer, living portion of each clone and separated by a 50 cm buffer. Plots were not chosen as part of a square because of the increased density of dead

stems in the clone centers due to clonal senescence (problem of nonhomogeneity).

The sampling protocol was the same for all sites. Arrangement of treatments was determined randomly for each plot within a quadrat or within each isolated clone. The treatments were time 1 and time 2. Time 1 included Plot A: cut to ground level and removal of all standing live and dead stems and litter; Plot B: cut and removal of all standing live stems; Plot C: cut and removal of all standing dead stems and litter; and Plot D: no treatment. Time 2 included Plot A: no treatment; Plot B: cut and removal of all standing dead stems and litter; Plot C: cut and removal of all standing live and dead stems and litter; and Plot D: cut and removal of all standing live and dead stems and litter.

The second treatment sampling (time 2) occurred 4 wk after the first sampling (time 1). The standing live, standing dead, and litter material for each plot in each sampling period were placed in separate, marked paper bags in the field and transported back to the laboratory. The plant material was dried at 75°C for 48 h and weighed. The data were converted to a 1.0 m² basis for later data analyses.

The arrangement of the plots allowed for production to be determined by several different methods (peak standing crop, Wiegert-Evans, and Lomnicki). In this study, the Lomnicki method (Lomnicki et al. 1968) was the preferred method for calculating net annual aboveground primary production (NAPP) because it has been found to give a more accurate estimate of NAPP than the other harvest methods (Shew et al. 1981; Kaswadji et al. 1990). In the Lomnicki method, net primary production for a given sampling period (NPP_i) was calculated by summing the growth of live material and the production of dead material (standing dead + litter). The growth of live material during a given sampling period was calculated by subtracting the dry weight mass (in grams) of the standing live stems in plot A (time 1) from the same dry weight mass found in plot D (time 2), or $\delta b_i = D_{\text{Live}} - A_{\text{Live}}$. Production of dead material during the sampling period was determined by adding the dry weights of standing dead stems and litter found in plot C at time 2 ($d_i = C_{2 \text{ dead stems}} + C_{2 \text{ litter}}$). NPP_i was the sum of these two factors ($\text{NPP}_i = \delta b_i + d_i$).

All of the sites were sampled six times during a 1-yr period, with each sampling period lasting for 4 wk, from a first (time 1) to a second (time 2) harvest. There were a total of 6 sampling periods, each having a duration of roughly 1 mo (total direct sampling of productivity = 6 mo). NAPP for each site was estimated by summing the NPP_i for the six sampling periods in which productivity was

measured directly and multiplying that sum for each site by 2 ($\text{NAPP} = \sum \text{NPP}_i \times 2$). Turnover rate for each site was calculated as the estimated NAPP divided by the peak standing live crop (Shew et al. 1981).

BELOWGROUND PRIMARY PRODUCTIVITY

Belowground productivity of *S. alterniflora* was measured using the ingrowth core bag technique during 2002 (Steen 1984; Vogt et al. 1998; Finer and Laine 2000). Belowground production was measured also in fall 2001, but did not include the C88 sites due to mechanical problems; only the 2002 data were used in subsequent analyses. In each site, three cores, consisting of burlap mesh bags (7.6 cm diameter × 30 cm depth) filled with sediment from a still unvegetated area in the youngest created site (C99), were placed haphazardly within homogeneous stands or along the outer edge of isolated clones (see above) of *S. alterniflora*. The sediment put into the core bags was the same dredge material used in forming the created sites (Proffitt and Young 1999; Penland 2001) and had similar structural characteristics (high clay and low sand contents) as the soils in the natural sites (Edwards and Proffitt 2003). It was assumed that possible differences in root growth patterns caused by core installation were minimized by the similarity between site soils and that used in the core bags. The core bag sediment was not sieved prior to filling the bags (Steingrobe et al. 2000).

Soil cores 30 cm deep (maximum observed root depth) were extracted in the sites by use of a corer. The sediment-filled mesh bags were then placed into the holes and left for 2 mo. After 2 mo, the bags were retrieved and transported back to the laboratory, where the cores were separated into three 10-cm intervals (0–10, 11–20, and 21–30 cm). Each interval was washed over a sieve (2.0 mm²), the belowground structures placed into marked paper bags, dried at 75°C for 72 h, and weighed. Total belowground dry weight (DW) for each core was calculated by summing the DW from the three depth intervals. Belowground DW was converted to a 1.0 m² basis for use in subsequent analyses. The percentage of belowground DW per depth interval was determined by dividing the DW of material in a given interval by total belowground DW for that core and multiplying by 100. The values from the three cores were averaged to calculate belowground biomass (g DW m⁻²) in each site for each sampling period.

Cores were put into the sites at quarterly intervals (once every 3 mo), but were left in the ground for 2 mo during each interval. The 2-mo period was deemed to be sufficient for adequate root growth into the bags but not too long for signifi-

cant death and decomposition to occur (Steen 1984). An individual sampling period lasted 2 mo.

In order to estimate net annual belowground primary productivity (NBPP) for each site, the four quarterly measures of belowground DW were added together. This sum for the 8 mo in which belowground productivity was measured directly was extrapolated to an annual estimation of NBPP by multiplying the sum in each site by 1.5.

STATISTICAL ANALYSES

Differences in the amount of aboveground and belowground biomass (g DW m^{-2}) between the natural and created sites were determined by nested analysis of variance (ANOVA), with sites nested within the type of site, being either natural or created. Square root or natural logarithm data transformations were done to achieve homogeneity of variance. These tests were conducted for all four sampling periods of the belowground data, but only for the aboveground data from August and December 2001, and February, April, and June 2002; only data from plot As were used in the aboveground analyses. This was done to determine whether there were any seasonal effects. Differences between the two natural sites were analyzed by *t*-tests, while one-way ANOVAs were run to test for significant differences among the created sites. Tukey's multiple comparison of means test was run if significant differences were found in the one-way ANOVA.

Two-way ANOVAs were run to test for differences in the proportion of belowground structures in each 10-cm depth interval among sites and between types (natural versus created), with site type and depth interval being the independent factors. If significant differences were found, then a similar analytical procedure to that used to test for differences in aboveground and belowground biomass (see above) was conducted for each 10-cm growth bag interval. Analyses were conducted for each sampling period.

Relationships between site age and the various aboveground biomass compartments (living, standing dead, litter, and total) were determined by regression analysis, following square root transformation to correct for normality problems. This allowed for evaluation of whether the biomass levels in the created sites approached natural ones as they aged. One-way ANOVAs were run on a data set including all of the sites to determine whether aboveground biomass levels were similar between the natural sites and the oldest created sites.

Differences in NAPP and NBPP among the sites appeared to be influenced by both site age and elevation. To test these observations, regression equations were calculated for these data following

natural log transformation. A stepwise procedure was used to determine which independent factors (site age, mean site elevation, site elevation range) were most important in affecting the two productivity measures. Age of the natural sites was given as 50 yr, which corresponds to the creation of the Calcasieu Ship Channel. This opening to the Gulf of Mexico increased salt water intrusion into the Hog Island area, transforming the previous brackish marsh systems into salt marshes (Proffitt and Young 1999; Penland 2001).

Relativized comparisons were conducted separately for NAPP and NBPP, following Zedler and Callaway (1999). The productivity values in the created marshes were divided by the mean value of the two natural marshes. The relative NAPP and NBPP values were each regressed against age of the created sites using the NONLIN program in SYSTAT (SYSTAT 2002). The time in years for the created marshes to have similar productivity levels as in the natural marshes was estimated from these regressions.

Unless stated, all statistical analyses were run using the general linear model program in SYSTAT, version 10.2 for Windows (SYSTAT 2002). An alpha level of 0.05 was used for determination of significant differences in all cases.

Results

ABOVEGROUND BIOMASS

Living *S. alterniflora* biomass (g DW m^{-2}) was present throughout the year in all of the sites, with maximum levels occurring in the summer (usually July or August) and minima in winter, usually February (Fig. 2). There was an opposite pattern for dead material, with the peak amount of standing dead matter occurring in winter. There was a distinct, short-lived peak (2–4 mo) in the amount of standing dead material in the youngest and oldest created sites (C83-green, C96E, C96W, C99). High levels of standing dead were found throughout most of the year in the natural and middle-aged created sites. The rapid production of new live material began in April or May in all sites.

Aboveground biomass levels for summer 2001 and 2002 were similar in the NAT2, C83-green, C93W, and both C96 sites. There was more living aboveground material in the NAT1 and C93E sites in 2001 than 2002, while the opposite was the case for the C83-60 m and C99 sites. There were indications that the NAT1 site was degrading, which may explain the lower biomass production measured in 2002. In summer 2001, the C83-60 m site was just beginning to recover from the previous year's dieback of *S. alterniflora*, resulting in low live biomass levels. Recovery had progressed much fur-

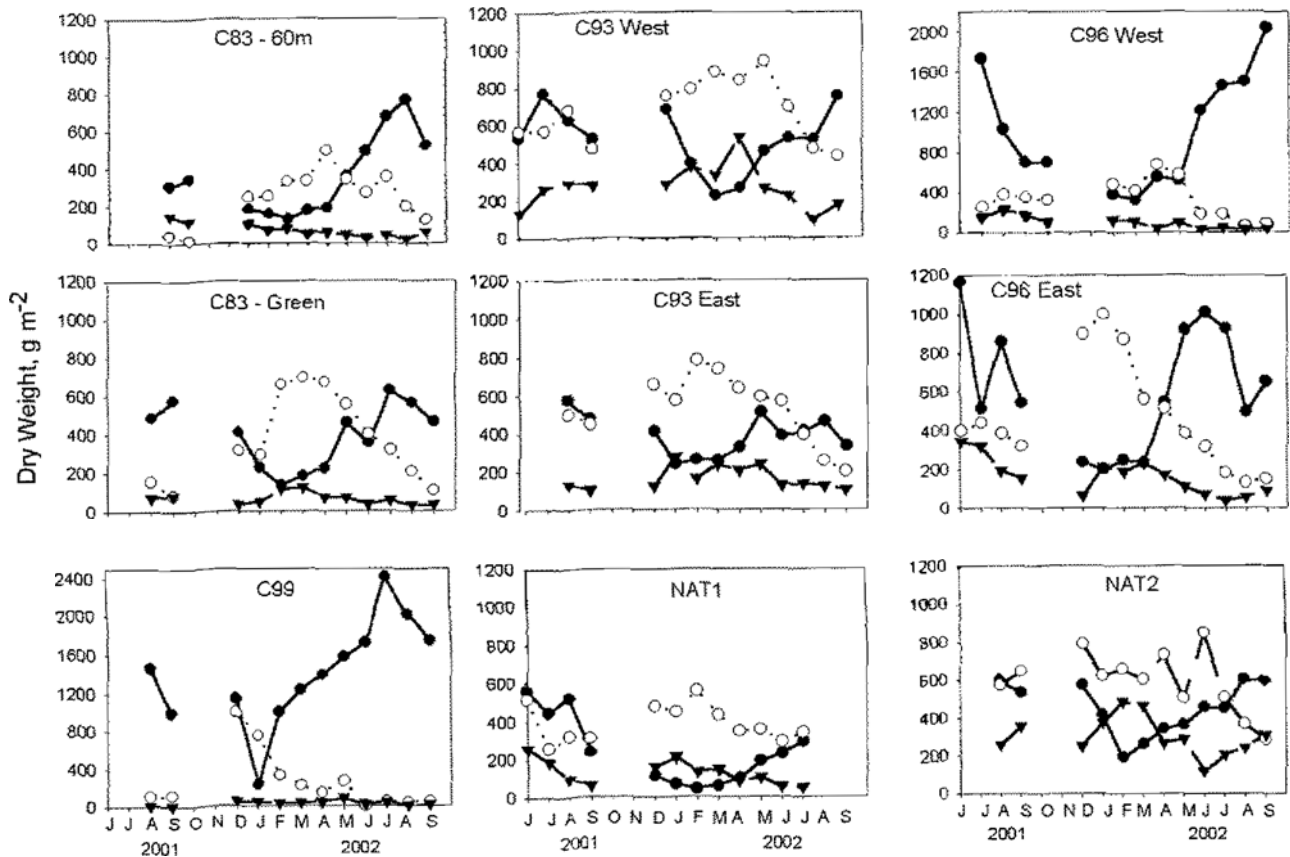


Fig. 2. Aboveground biomass (g DW m⁻²) allocation in all months (x axes) for which samples were collected for all study sites. Site acronyms are as mentioned in the text. Closed circles = live shoots, open circles = dead standing shoots, and closed inverted triangles = litter.

ther by summer 2002, resulting in the subsequent greater live biomass. The differences in biomass levels for the C98E and C99 sites may be age related (see below).

Differences in total (live + dead) aboveground biomass of *S. alterniflora* between the natural and created sites were not significant, based on the results from the nested ANOVAs. The amount of live biomass differed significantly in most of the sampling periods tested (August and December 2001 and February, April, and June 2002). Except for August 2001, there was significantly greater live aboveground biomass in the created marshes compared to the natural marshes (Fig. 2). The plots in the natural sites contained more dead material. In cases where the two natural sites differed significantly, NAT2 > NAT1 in all situations (*t*-tests, *p* < 0.02).

The amount of live stem material in the created sites was negatively related to site age. This was best expressed as an exponential relationship (live biomass = $ae^{-b \text{age}}$; *a* = y-intercept, *b* = slope) with *r*² > 0.50 except in December (*r*² = 0.22), probably as a result of stem senescence producing more

equal conditions among the sites (Fig. 3). Live biomass levels in the older C83 and C98 sites were similar to those of the natural sites, except in February and April 2002, when live biomass levels in the NAT1 site were significantly lower than in the others.

There were significant quadratic relationships between the amount of standing dead and litter biomass with site age of the created marshes. The middle-aged C98 and C96 sites had greater amounts of dead material than either the oldest or youngest sites. Standing dead and litter biomass levels were similar between the natural and C83 sites for all of the months analyzed.

ABOVEGROUND PRODUCTIVITY

NAPP ranged from about 1640 to 3570 g DW m⁻² yr⁻¹, when estimated using the Lomnicki method (Fig. 4). The C93W site was most productive, followed by C96W and C99. The eastern halves of the C93 and C96 created sites, as well as the NAT1 natural marsh, were the least productive, with NAPP < 2,000 g DW m⁻² yr⁻¹. The other natural site (NAT2) and the two C83 sites were inter-

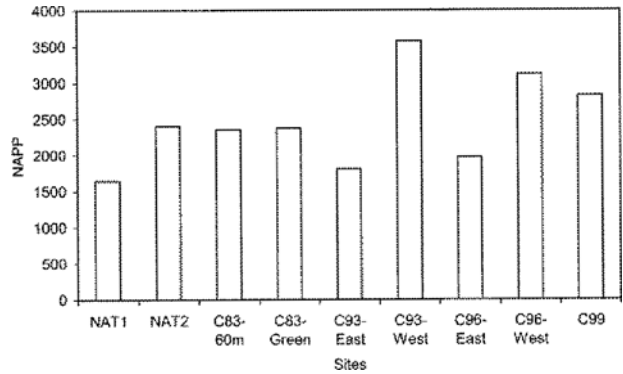
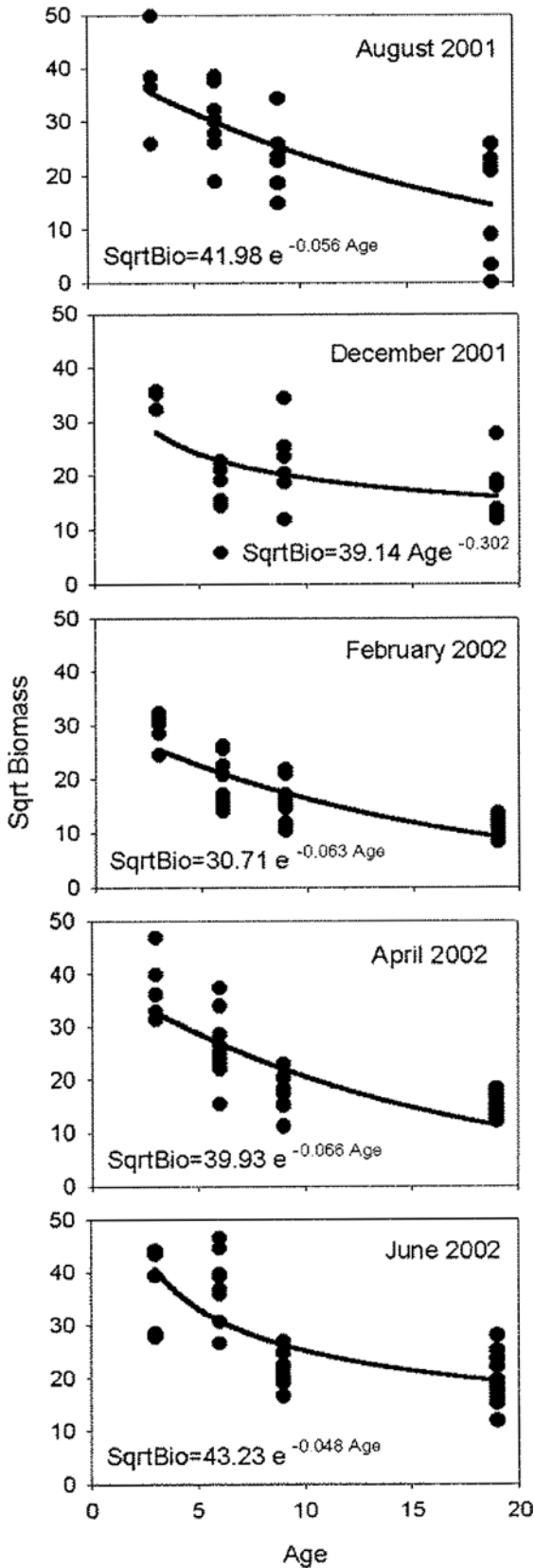


Fig. 4. Estimated net aboveground primary productivity (NAPP) of *Spartina alterniflora* in the study sites, using a modified Lomnicki method. Estimated annual productivity was calculated by summing the net productivity of the six sampling periods and then extrapolated to a full year by multiplying the sums by 2.

mediate (Fig. 5). The estimated NAPP for the C93W site was high because of high stem mortality within several of the sampling periods. This mortality was most likely followed by the growth of new live shoots, as shown by the high turnover rate for this site (Table 2).

NAPP was significantly and negatively affected by both site age and site elevation range ($\ln\text{NAPP} = 8.311 - 0.015 \times \text{RANGE} - 0.011 \times \text{AGE}$, $r^2 = 0.735$, $F_{2,6} = 12.11$, $p = 0.008$). The youngest sites were most productive with the oldest created sites having the same productivity as at least the NAT2 site. NAPP was significantly lower in those created sites with a more heterogeneous topography (C93E and C96E).

A further regression analysis was conducted on sites with elevational ranges <20 cm (excluding C93E and C96E). This was done to determine whether site age influenced NAPP among sites with equivalent elevational ranges. Most of the sites also had similar mean elevations (Table 1). There was a borderline significant negative relation between NAPP and site age ($\ln\text{NAPP} = 8.058 - 0.010 \times \text{Age}$, $r^2 = 0.521$, $F_{1,5} = 7.53$, $p = 0.041$). There was a trend towards decreased NAPP as sites with similar elevations aged.

BELOWGROUND PRODUCTIVITY

NBPP for *S. alterniflora* ranged from less than 1,900 to almost 3,600 g DW m⁻² yr⁻¹ (Fig. 5). The

Fig. 3. Regression analyses relating living aboveground biomass (g DW m⁻²) in the created sites to their age since being constructed. Square root transforms done to achieve homogeneity of variance. Biomass data were the same data used in the nested ANOVAs (see Fig. 4).

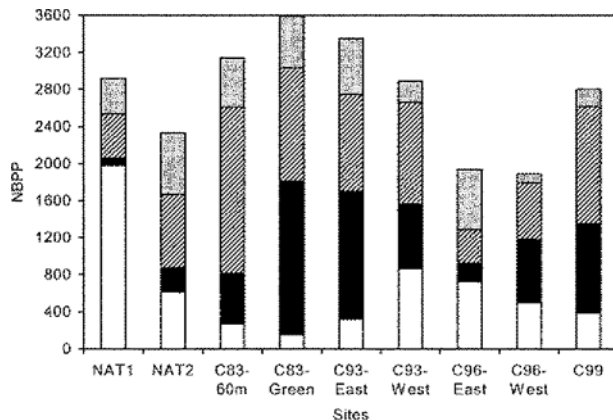


Fig. 5. Estimated net belowground primary productivity (NBPP) of *Spartina alterniflora* in the study sites calculated from the four 2002 sampling periods only. Bars: white = January–March; black = April–June; diagonal stripes = July–September; and gray = October–December. Bar height for each site is equal to the estimated annual NBPP.

relation between NAPP and NBPP (root:shoot ratios) for each site is given in Table 3. For the most part, NBPP was greatest in the oldest created sites, with C83 and C93E sites being the only marshes with NBPP > 3,000 g DW m⁻² yr⁻¹, while NAT1 had an NBPP just below that level. The younger C96 sites produced the least amount of belowground structures, with NBPP levels <2,000 g DW m⁻² yr⁻¹. The youngest site (C99) was more productive belowground than the older NAT2 site. Site age did not significantly influence NBPP, even though there was an observable increasing trend in NBPP with created site age (Fig. 5). There was a significant, albeit weak, relationship to mean site elevation ($\ln\text{NBPP} = 8.522 - 0.009 \times \text{Mean Elevation}$, $r^2 = 0.544$, $F_{1,7} = 9.34$, $p = 0.022$) following removal of a possible outlier site (C96W).

As with NAPP, NBPP was analyzed further to test whether production of belowground structures in sites with equivalent elevations changed as they

TABLE 2. Shoot turnover rate of *Spartina alterniflora* in the Sabine National Wildlife Refuge study sites, southwest Louisiana. Turnover rate = net aboveground primary production (NAPP g DW m⁻² yr⁻¹)/peak standing crop (g DW m⁻²), as given in Shew et al. (1981).

Site	NAPP	Peak Standing Crop	Turnover Rate
NAT1	1642.56	561.74	2.92
NAT2	2399.82	607.44	3.95
C83-60m	2354.46	768.47	3.06
C83-Green	2373.40	627.59	3.78
C93E	1803.68	572.94	3.15
C93W	3573.82	754.91	4.73
C96E	1966.02	1168.03	1.68
C96W	3112.16	2036.16	1.53
C99	2817.85	2406.81	1.17

aged. The same sites were used in this analysis as were included for the NAPP analysis, except for C96W, which was found to be an outlier. Contrary to the results for NAPP, no significant relationship was found between NBPP and site age ($\ln\text{NBPP} = 8.171 - 0.004 \times \text{Age}$, $r^2 = 0.028$, $F_{1,4} = 1.15$, $p = 0.345$).

There were few significant differences in NBPP levels between either the natural and created sites or among the sites within each category for any of the quarterly sampling periods. Any differences occurred early in the year. Natural sites produced greater belowground biomass than the created sites in the first quarter of 2002 (January–March: nested ANOVA, $F_{1,16} = 9.77$, $p = 0.007$), due to the very high production seen in the NAT1 site. The reverse was true in the second quarter (April–June: nested ANOVA, $F_{1,16} = 19.46$, $p < 0.0005$), with the C83-green and C93E sites producing almost 1,000 g DW m⁻² during this period while there was little production in either of the natural sites. The only significant difference found among the sites was in the first quarter, when belowground production in NAT1 > NAT2 ($T = 3.37$, $p =$

TABLE 3. Root:shoot ratios (R:S) of *Spartina alterniflora* for the natural (NAT) and created (C) sites at Sabine National Wildlife Refuge, southwest Louisiana. R:S ratios for each site were calculated by dividing the net aboveground primary productivity (NAPP) by the net belowground primary productivity (NBPP) for the respective sites. The 2002 belowground values were estimated from data collected from sampling periods in 2002 only, while the 2001–2002 values were estimated including data from the October–December 2001 sampling period. The C83 sites were not measured in the October–December 2001 period because of mechanical problems. See text for details.

Site	NAPP	NBPP 2002	R:S 2002	NBPP 2001–2002	R:S 2001–2002
NAT1	1642.56	2917.72	1.78	11247.78	6.85
NAT2	2399.82	2331.76	0.97	5042.98	2.10
C83-60m	2354.46	3141.24	1.33	—	—
C83-green	2373.40	3589.48	1.51	—	—
C93E	1803.68	3349.28	1.86	4754.69	2.64
C93W	3573.82	2888.29	0.81	5472.09	1.53
C96E	1966.02	1937.98	0.98	4974.93	2.53
C96W	3112.16	1888.41	0.61	3373.17	1.08
C99	2817.85	2799.86	0.99	3636.41	1.29

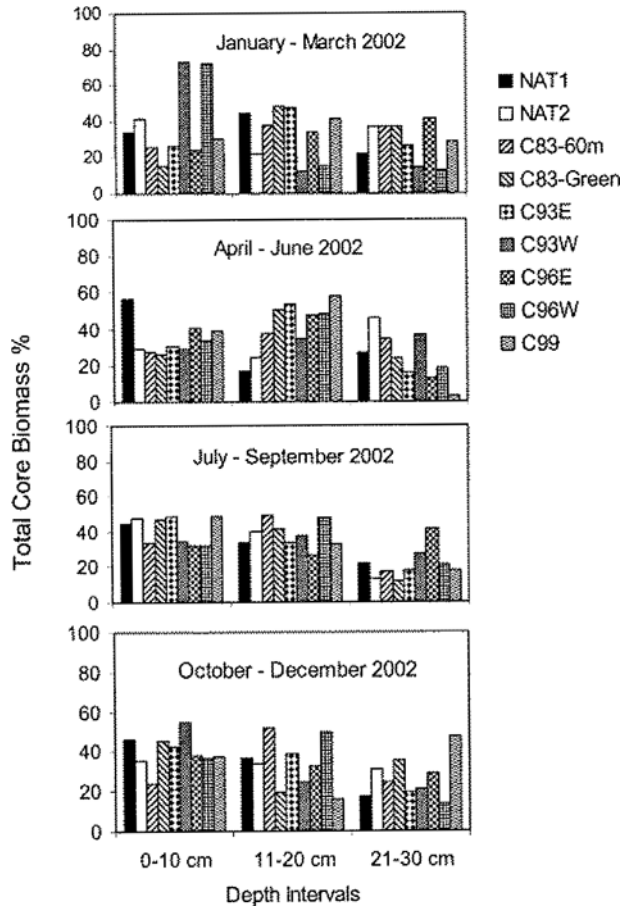


Fig. 6. Distribution of live belowground structures of *Spartina alterniflora* (as the percent of mean total belowground biomass, g DW m^{-2}) in the natural and created salt marsh sites for the four sampling periods in 2002. The dotted line denotes the 50% distribution mark.

0.043); differences were never significant among the created sites.

Although not included in the statistical analyses of NBPP, because not all sites were sampled, the measurements from the earlier October–December 2001 sampling period showed some interesting contrasts with those from the same time period in 2002. Belowground production was much higher in all of the sites sampled compared to the 2002 measures from the same quarter and in some cases equaled or surpassed NBPP for the entire 2002 sampling period (data not shown). The NAT1 site was significantly more productive than the other sites, with an estimated belowground productivity for the 2-mo period of $5,800 \text{ g DW m}^{-2}$.

Belowground structures of *S. alterniflora* were found in all three depth intervals for all sites, with the majority of biomass occurring below 10 cm depth. There were few significant differences in

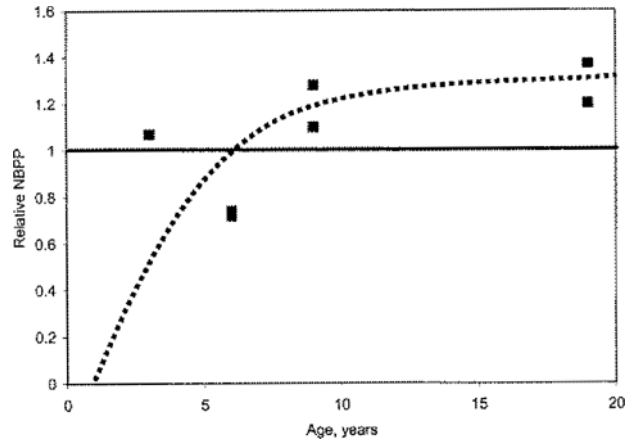


Fig. 7. Relatized comparison of NBPP of *Spartina alterniflora* in differently aged created salt marshes to mean productivity values for the two natural reference marshes. The regression curve (dotted line) is relative NBPP = $0.583 + 0.523 \times \log_{10} \text{Age}$.

the root and rhizome depth profiles between the created and natural sites or among sites within each site type (Fig. 6). There was a significant site type (created versus natural) by depth interaction for the April–June sampling period due to the significantly greater proportion of belowground biomass at the intermediate depth interval (11–20 cm) in plants growing in the created sites. No significant differences were found in proportion levels between the two natural sites in all sampling periods. For the created sites, plants in the C93W and C96W sites had a significantly greater proportion ($F_{6, 13} = 5.39$, $p = 0.005$) of belowground structures in the uppermost (0–10 cm) interval during the first sampling period (January–March 2002). The proportion of belowground structures in the deepest interval (21–30 cm) was significantly greater for plants in the C96E site than in the other created sites during the July–September 2002 period.

RELATIVIZED COMPARISONS

There was a decreasing linear trend in relative NAPP as the created marshes aged. The decrease was not significant ($F_{1, 5} = 0.25$, $p = 0.64$, $r^2 = 0.05$), meaning that there has been little change in the aboveground productivity (m^2 basis) of the created marshes as they age, relative to the natural marshes. At this rate, it would be 35 yr before the created marshes had NAPP levels similar to those found in the natural marshes.

Relative NBPP increased exponentially in the first few years after site creation, but then reached an asymptote starting in year 9 (Fig. 7). The resulting nonlinear regression curve was significant

($F_{2,5} = 81.80$, $p < 0.001$; $r^2 = 0.35$). The slope of the asymptotic part of the curve was not significantly different from zero, but there was still an increasing trend (relative NBPP = $1.10 + 0.01 \times \text{Age}$). Equivalence for belowground productivity was reached between 6 and 8 yr after site creation, but then exceeded levels in the natural marshes.

Discussion

The main assumption behind the idea of trajectories in terms of ecological restoration projects is that the structure and functions of the created sites should begin to approximate those in natural reference habitats over time (Simenstad and Thom 1996; Zedler and Callaway 1999; Morgan and Short 2002). Indicator factors, such as primary productivity, may be chosen and measured to determine whether a particular creation or restoration project is successful (Short et al. 2000; Streever 2000). The objective of this study was to determine whether net aboveground and belowground productivity of *S. alterniflora* in created and natural reference salt marshes in the Sabine NWR became similar as the created marshes aged.

Both aboveground and belowground productivity in the created and natural salt marshes became more similar over time. There was a trend of decreasing NAPP as the created marshes aged, but these levels were still well above the mean NAPP values of the natural marshes, as shown by the relativized comparison. Equivalency in NAPP has not been reached after almost 20 yr since marsh creation. At the same time, NBPP increased from the younger to the older created sites, reaching levels equivalent to those in the natural sites after 6–8 yr since marsh creation, but then surpassed levels found in the natural marshes. The lack of equivalency in primary productivity, and the estimated decades-long time (35 yr) for equivalency to occur for NAPP, is similar to the lack of equivalency found for certain soil structural characteristics, especially percent organic matter, measured in these same sites (Edwards and Proffitt 2003). Such a relationship between *S. alterniflora* productivity and soil organic matter development has been observed in other salt marsh restorations (e.g., Webb and Newling 1985; Craft et al. 1999).

One possible reason for the slow rate at which the created marshes in our study attain equivalency with the natural marshes regarding NAPP may be that the Lomnicki method incorporates both live and dead biomass when estimating net primary productivity (Lomnicki et al. 1968). Live aboveground biomass in the created sites became similar to those in the natural marshes 19 yr after marsh creation. No such relationship was evident for the dead (standing dead and litter) biomass, with the

natural sites always having higher levels of dead aboveground biomass. The incorporation of the dead biomass in the Lomnicki calculations may have offset the effect of the live biomass relationship with age, resulting in the perceived lack of equivalency to date.

To test this, NAPP was reestimated using the Wiegert-Evans method (Wiegert and Evans 1964), another harvest technique that does not include dead biomass in its calculations. The resulting negative cubic relativized relationship (data not shown) was different from that estimated by the Lomnicki method. Similar to the Lomnicki results, no equivalency was found 19 yr after marsh creation when NAPP was estimated by the Wiegert-Evans method.

The manner in which the relativized comparisons were determined may not have shown an equivalent trajectory in NAPP between the created and natural marshes because, while *S. alterniflora* was clearly the dominant in the natural and older (C88 and C98) created marshes, there were only isolated clones in the younger (C96 and C99) marshes. Whole-site productivity would be less in these younger sites than calculated. Relative NAPP was recalculated after dividing the NAPP for the C96 and C99 sites by 2 to represent *S. alterniflora* covering at most only 50% of the area of these marshes. This produced a quadratic curve (data not shown) but still no equivalency 19 yr after the created marshes were formed. Although there were specific differences among the methods of calculating NAPP equivalency, in general all of the methods used showed that NAPP still differed between the created and natural marshes 19 yr after marsh creation.

NAPP levels of *S. alterniflora* in our study sites were similar to those found in other natural Louisiana salt marshes (Kirby and Gosselink 1976; White et al. 1978; Hopkinson et al. 1980; Kaswadji et al. 1990). NAPP in these studies ranged from 750 to 2,600 g DW m⁻² yr⁻¹, depending on the method used. Kaswadji et al. (1990), using the Lomnicki method as in our study, estimated NAPP in a natural Louisiana marsh to be 2,050 g DW m⁻² yr⁻¹, which is similar to the mean NAPP value of the two natural sites in our study. This was the value used in determining the relativized production comparison.

In contrast to our sites, primary productivity in created salt marshes became similar to that in natural marshes in North Carolina within 3 yr after marsh construction (Craft et al. 1999). Aboveground biomass of *S. alterniflora* in these marshes ranged from almost 650 to 870 g m⁻², which were within the range of living aboveground biomass in our sites. The faster time to equivalence in the

North Carolina salt marshes, compared to our sites, may be because *S. alterniflora* was transplanted in the North Carolina sites (Craft et al. 1988) while it established by natural colonization in the Sabine NWR sites (Edwards and Proffitt 2003). Transplanting should lead to more rapid marsh development than natural colonization, the rates of which can vary widely (Broome et al. 1988). Usually, *S. alterniflora* colonized the inner portions of our sites 1–2 yr after marsh creation and became dominant after 5 yr (Edwards and Proffitt 2003).

The majority of belowground biomass was found below the 0–10 cm depth interval in our study sites, which is similar to the results of other studies from the southern U.S. (Schubauer and Hopkinson 1984; Seliskar et al. 2002). Clones from more northern latitudes have more shallow depth profiles (Valiela et al. 1976); this difference appears to be genetic and not just a response to different environmental conditions (Seliskar et al. 2002).

Belowground production in our sites was within the range of NBPP reported for other studies of *S. alterniflora* from the Atlantic and Gulf of Mexico coasts (Gallagher 1974; Valiela et al. 1976; Howes et al. 1985; Blum 1993; Turner et al. 2004). Many of these studies included both live and dead material when calculating belowground production, while only live material was used in our estimations of NBPP. If only live material is compared, then our natural and created sites had greater belowground production compared to the marshes of these other studies. This is especially evident when the 2001 data are included in our NBPP calculations. Most of the other studies are from more northern areas with cooler climatic conditions, resulting in lower biomass production. Belowground production in most of the Sabine sites were more similar (albeit still higher) to those from healthy Louisiana salt marshes studied by Turner et al. (2004).

There was an apparent elevational effect on *S. alterniflora* productivity in the study sites, with NAPP being negatively related to the amount of topographic heterogeneity in a site while there was a negative relation between mean site elevation and NBPP. Based on their elevations, the Sabine sites would be classified as occurring in the low marsh zone, with greater productivity than plants growing in the high marsh zone (Ellison and Bertness 1986). NAPP in these sites was similar to that in low marsh areas of other marshes, except for the NAT1, C93E, and C96E sites. The low productivity of the NAT1 site may be due to marsh degradation (Edwards and Ford personal observation). Various other ecological factors may act to reduce *S. alterniflora* productivity in C93E and C96E. Greater topographic heterogeneity would al-

low for a larger number of species to colonize and establish in the marsh. The importance of small changes in elevation in affecting plant species composition is well known for coastal marshes (Gosselink 1984; Webb and Newling 1985; Landin et al. 1989; Chabreck 1994; Dawe et al. 2000). It is possible that some of these species may outcompete *S. alterniflora*, reducing that species' productivity under the particular site conditions. The high marsh species, *S. patens* and *D. spicata*, as well as the shrubs *Iva frutescens* L. and *Baccharis halimifolia* L., are codominants with *S. alterniflora* in both sites (Edwards and Proffitt 2003). The low nutrient conditions of the created sites (Mills unpublished data) may also decrease the competitive ability of *S. alterniflora* in favor of other species (Bertness 1991).

Abiotic stressors, such as salinity or lower soil moisture levels, may interact with biotic factors in depressing the production of belowground structures in C96E (Turner et al. 2004). Flood events, which remove accumulated salts (Gosselink 1984; Mitsch and Gosselink 2000), were less common in this site than in C93E (Edwards unpublished data) because of its higher elevation. Increased stress from high salinity levels will lead to reduced growth of *S. alterniflora* and decreased productivity (Bradley and Morris 1991; Morris et al. 2002).

It is possible that site age \times elevation interactions may be important in affecting *S. alterniflora* productivity. This would be important information needed for predicting the success of future restoration projects. Such an interaction could not be ascertained from this particular study.

CONCLUSION

Physical characteristics of a salt marsh, such as soil type, elevation, and hydrology, provide the template on which communities develop and ecosystems function. Once the template is set, then biotic factors, interacting with these physical factors, strongly determine ecosystem structure and functioning (Roberts 1987; Allen and Hoekstra 1992). Over the long term, biotic processes interact with physical factors, such as sediment accretion rates, to affect marsh elevation, which may result in a stable marsh system in relation to relative sea level rise (Morris et al. 2002). At shorter time scales, current marsh elevation can affect biotic factors, such as plant zonation (Bertness 1991) and primary productivity (Mendelsohn and Morris 2000; Morris et al. 2002). In addition to these, salt marsh structure and functions are affected by biota \times biota interactions, such as competition (Bertness 1991) and facilitation (Egerová et al. 2003).

The differences in NAPP and NBPP between the natural and created salt marshes suggest that equi-

alency has not been reached even after almost 20 yr since the oldest created marsh was constructed. Several decades (an estimated 35 yr) may be required after marsh creation for aboveground productivity to be similar in natural and created marshes, based on the relativized comparison analyses. Belowground productivity appears as though it may remain higher in the created marshes as they age, compared to the natural salt marshes. Future productivity measurements will be needed, at a maximum 5-yr interval, to determine whether or when equivalency is attained.

Space-for-time substitution is a commonly used method for evaluating the success of restoration and creation projects (Michener 1997; Molnar and Botta-Dukat 1998). This method is not appropriate where the sites being evaluated have different life histories. All of the created sites in the Sabine NWR were constructed in previously open water areas by the placement of dredged material, which was supplied from the same source, so space-for-time substitution is a suitable evaluation method for these created marshes. In sites with similar elevations, aboveground production decreased as the created sites aged, approaching levels found in natural marshes. The lower productivity of *S. alterniflora* found in some of the created marshes of the same age was due to their having higher final elevations. This underscores the importance, when creating or restoring salt marshes, of having physical traits that are similar to those of natural reference marshes in order for the restoration to be successful (Vance et al. 2003). Even then, decades may need to pass before equivalency between the created and natural marshes is reached.

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- FORD, M. personal observation. Coalition to Restore Coastal Louisiana, 746 Main Street, Suite B101, Baton Rouge, Louisiana 70802.

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