Wetlands Ecol Manage (2010) 18:111–117
DOI 10.1007/s11273-008-9124-4

ORIGINAL PAPER

Implication of nutrient and salinity interaction on the productivity of *Spartina patens*

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Received: 14 February 2007 / Accepted: 17 October 2008 / Published online: 1 November 2008

Abstract Reintroduction of fresh water to coastal systems with altered hydrologic regimes is a management option for restoring degraded wetland habitats. Plant production in these systems is believed to be enhanced by increased nutrient availability and reduced salinity. Although studies have documented nutrient limitation and salinity stress in coastal marshes, interpreting the effects of freshwater reintroduction on plant production is difficult because high nutrient availability often is confounded with low salinity. We tested the hypothesis that plant growth response to nutrients does not vary with salinity in a greenhouse study. Treatments consisted of four nutrient concentrations and four non-lethal salinity levels; plant response was measured as biomass accumulation after 144 days of exposure. The significant interaction between salinity and nutrient concentrations indicates that response of *Spartina patens* marshes to freshwater inflows would vary by site-specific soil conditions. Biomass decreased with increased salinity at all four nutrient concentrations with variation among the nutrient concentrations decreasing as salinity increased. We demonstrate the importance of considering ambient salinity and nutrient soil conditions in restoration planning involving freshwater inflow. We propose salinity should remain a primary concern in restoration plans targeted at improving degraded *S. patens*-dominated marsh habitat.

Keywords Salt stress · Nutrient limitation · Marsh accretion · River reintroduction

Abbreviations

ANOVA	Analysis of variance
ppt	Parts per thousand

Introduction

Restoring fresh water flow is increasingly used as a wetland restoration technique in areas where the natural flooding regime has been altered (Army US Corps of Engineers (USACE) and Louisiana Department of Natural Resources (LDNR) 2004). Hydrologic alterations that restrict lateral movement of water or prevent overbank flooding may increase stress and limit resources for coastal marsh plants (Swenson and Turner 1987; Reed et al. 1997).

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Increased salinity can reduce biomass of coastal marsh macrophytes (Bradley and Morris 1992; Broome et al. 1995), and restricted nutrient input can reduce plant productivity, decreasing marsh vertical accretion (McCaffery and Thompson 1980; Bricker-Urso et al. 1989; Turner et al. 2000; Chmura and Hung 2004; Nyman et al. 2006). Reintroducing freshwater is thought to increase plant production by reducing salinity and increasing nutrient availability (DeLaune et al. 2003; Army US Corps of Engineers (USACE) and Louisiana Department of Natural Resources (LDNR) 2004).

Understanding the effect of freshwater reintroduction to marsh plant production is key to determining ecological impacts and best restoration practices. When freshwater inflow is restored, plant response resulting from changes in nutrient availability can be difficult to distinguish from that caused by alteration of the salinity regime (e.g., Lane et al. 1999; Alexander and Dunton 2006). When rivers are the source of freshwater, the magnitude of salinity change is greater than the change in nutrient concentration (e.g., Lane et al. 1999); the reverse is true, however, when treated wastewater effluent is the source (Alexander and Dunton 2006). Predicting the size and magnitude of effected area (where plant growth will respond to freshwater reintroduction), requires understanding how nutrient availability and salinity stress affect plant growth. River reintroductions to coastal marsh where plant growth is limited primarily by high salinity may affect a large area because it is more likely that soil salinity conditions would be altered more than nutrient concentrations. Studies designed to test the relative importance of nutrient resources and salinity stress will improve understanding of spatial and temporal variability in the productivity of coastal marsh macrophytes, and the management and restoration of coastal marshes.

Also referred to as “river diversions,” we use the term freshwater reintroduction because the method is applicable to more than riverine systems and the term “diversion” implies an unnatural hydrologic alteration. Freshwater reintroductions may involve freshwater sources, such as lake water, and mimic or restore natural hydrology. Plans to offset wetland loss in Louisiana have favored utilizing the nutrient loaded Mississippi River water for reintroductions (Army US Corps of Engineers (USACE) and Louisiana Department of Natural Resources (LDNR) 2004), although lake waters with much lower nutrient concentrations than the Mississippi River have also been used for reintroductions to southwestern Louisiana marshes that are far from rivers. Even among freshwater reintroductions that use river water, nutrient load can vary with technique. Siphons utilize the upper column of the river only during spring floods. In contrast, gates allow introduction of water from lower in the water column year round and probably discharge heavier sediments more than siphons. Sediments can also be pumped directly from the river bottom into marshes to increase elevation and nutrient availability. Treated wastewater was used in a freshwater introduction to a hypersaline area (Alexander and Dunton 2006). The impact of the Caernarvon freshwater reintroduction in southeastern Louisiana, which is the largest freshwater diversion from the Mississippi River, has been examined with regard to water quality, submerged aquatic vegetation, nekton, soil quality, and marsh vertical accretion (Lane et al. 1999, 2004; DeLaune et al. 2003; Rozas et al. 2005; Wissel et al. 2005), but it remains to be seen how those results relate to other existing and potential freshwater reintroduction projects.

Spartina patens (Ait.) Muhl. dominates large areas of brackish coastal marsh throughout the Atlantic and Gulf of Mexico coasts of North America, and is the most common emergent plant in Louisiana’s 16,000 km^2 coastal wetlands (Chabreck 1970). The lethal salinity for *S. patens* varies from 65 to 95 ppt among different populations, although stress occurs at a lower but unspecified salinity level (Hester et al. 1996). In a greenhouse experiment, this species had higher biomass in salinity treatments of 0 and 7 ppt compared to that in 14, 21 or 28 ppt salinity treatments (Ewing et al. 1995). La Peyre et al. (2001) found no effect of salinity on growth between 0 and 8 ppt in a greenhouse experiment. In another greenhouse study, DeLaune et al. (2005) found that adding nutrients (10.0, 8.7, and 15.6 g N m^{-2}) increased biomass of *S. patens*, but lowering salinity from 8 to 0 ppt did not. Those findings indicate that increased *S. patens* production resulting from freshwater reintroduction to brackish marsh would likely be limited to the area that receives nutrients (i.e., nutrient outfall area), rather than the larger area where salinities are reduced. In a field experiment within *S. patens*-dominated marshes, Foret (2001) examined the response of plants in high (13–25 ppt) and low (0–4 ppt) salinity marshes to nitrogen and phosphorus additions (36 g N m^{-2} year^{-1}, 2 g P m^{-2} year^{-1}). In that study, adding nutrients increased biomass only at the low salinity sites, indicating that salinity was the primary limiting factor and nutrients were secondary. Those findings indicate the benefit from a freshwater reintroduction would extend beyond the nutrient outfall area to encompass the larger reduced salinity zone.

We conducted a greenhouse experiment to determine the conditions under which salinity and nutrients are primary and secondary limiting factors to growth of *S. patens*. We tested the hypothesis that plant growth response under various nutrient conditions does not vary with salinity.

Methods

The experimental design included four levels of salinity, four levels of nutrients, and eight replicates. The soil used was a homogenous mixture of 90% commercial sand and 10% potter's clay. Nutrient treatments were one of four combinations of 19–5–8 and 35–0–0 encapsulated N–P–K slow release fertilizer mixed with the soil. The nutrient treatments were designed to approximate 25, 75, 125, and 200% of the average nitrogen and phosphorus levels in the soils of unmanaged, *S. patens*-dominated marshes at Rockefeller Wildlife Refuge in southwestern Louisiana (Table 1), which Foret (2001) determined as 2.009 mg N cm^{-3} and 0.1022 mg P cm^{-3}.

Spartina patens was vegetatively propagated in separate bedding trays that contained sand, water and commercial fertilizer (Peters 20–20–20 N–P–K). We replicated with two populations of *S. patens* that differ in their response to salinity. Hester et al. (1996) showed that one population had a lethal salinity (defined as 50% death of aboveground tissue) of 66 ppt but that another population had a lethal salinity level of 81 ppt. Plants from these different populations, rather than plants from different locations, were used as replicates to avoid the remote possibility that plants collected from different locations were actually clones produced by vegetative growth. We neither intended nor designed our experiment to compare the response of our replicates to our treatments. By using the two populations, we incorporate natural variation and decrease the likelihood of a type two error.

On 16 June 2001, two ramets from each population were transplanted to 64 one-gallon (7.25 × 17.145 cm) pots of experimental soil for a total of 128 pots. All sand was washed from the plants before transplanting. Two pots, one of each population, were placed in 64 tubs (60.7 × 40.4 × 31 cm) and flooded with well water (0.12 ppt salinity) to the soil surface.

After a 26-day acclimation period in the experimental soils, we applied the salinity treatments. Forty Fathoms marine mix (bioassay grade) was added to the tub water in five installments over a 10 day period until the target salinity levels of 2, 6, 18, and 36 ppt were reached. After the final salt addition, the tubs were randomly arranged spatially to reduce any proximity effects caused by light and temperature variations. We added water twice each week to replace water lost via evapotranspiration. Also, water from the tub was poured over the top of the soil in each pot twice a week to reduce salt accumulation in the soil.

Every 3–4 weeks salinity and conductivity were measured in the 64 tubs of water. Porewater samples also were collected from a randomly selected subsample of 16 pots and measured for salinity (one from each treatment level).

Table 1 Concentration of nitrogen (N) and phosphorus (P) used in experimental treatments relative to two comparable records

Treatment	Concentration (mg cm^{-3} of soil)		Percent of Rockefeller refuge[a] average		Percent of coastal Louisiana[b] average	
	N	P	N (%)	P (%)	N (%)	P (%)
Lowest	0.49	0.024	24	23	32	124
Low	1.46	0.073	79	71	95	376
Medium	2.43	0.12	121	117	158	618
High	3.89	0.19	194	186	254	978

[a] Foret (1997)

[b] Bruphacher et al. (1973)

The experiment was ended on 6 November 2001, 144 days after initiating the nutrient treatments. Aboveground and belowground biomass was harvested over a 3 day period. Belowground biomass was separated from aboveground biomass and washed. All biomass was dried at 60°C to a constant weight, and weighed.

Preliminary analyses were conducted using analysis of variance (ANOVA). We tested for differences in biomass among the combinations of salinity and nutrient treatments using Proc Mixed (Proc Mixed, SAS version 9.1, SAS Institute Inc., Cary, NC, USA). Nutrient concentration, salinity, and their interaction were in the model statement, with an alpha level of <0.05. The residuals were not normally distributed, so we used a square root transformation that corrected the distribution for the analysis. We present untransformed data in figures. Residuals were not homogeneous for salinity treatments. We used the mixed procedure option because it allows analysis with heterogeneity of variance by partitioning the mean square error by treatment. Instead of the standard fixed effect and interaction term variances divided by the interaction error term, the mixed procedure also allows partitioning the variance by a specified error term. The experiment included eight replicates for each salinity/nutrient combination. However, these were paired by population (into tubs) and therefore not independent, so the proper error term is the nutrient and salinity interaction within pairs (tubs) as the random effect. In the mixed procedure, data were grouped by salinity to partition the unequal variances, and nutrient and salinity interaction within tub was used in the random statement to correct the error term.

Table 2 Statistic results of analysis of variance on four salinities, four nutrient concentrations, and their interaction

Effects	Num DF	Den DF	*F* value	Probability >*F* value
Nutrient	3	48	20.26	<0.0001
Salinity	3	48	119.22	<0.0001
Nutrient × salinity	9	48	2.52	0.0188

Num DF Numerator degrees of freedom, *Den DF* Denominator degrees of freedom

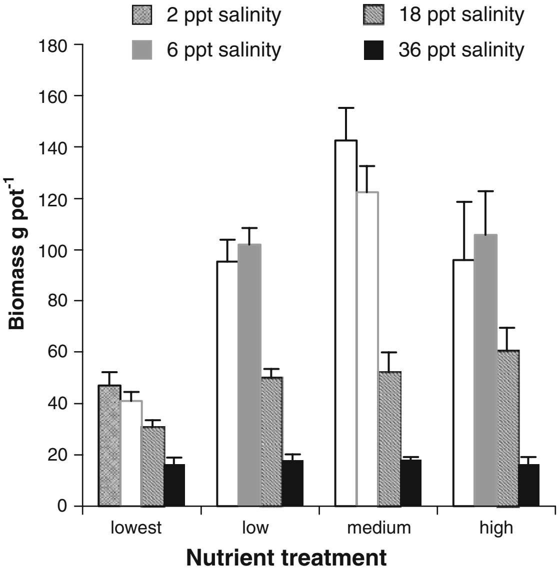

Fig. 1 Mean biomass of *Spartina patens* by salinity with standard error bars in a greenhouse experiment in which water salinity and nutrient concentration varied among 128 pots. Nutrient treatments were (*lowest*) 0.49 mg N cm^{-3} and 0.024 mg P cm^{-3}, (*low*) 1.46 mg N cm^{-3} and 0.073 mg P cm^{-3}, (*medium*) 2.43 mg N cm^{-3} and 0.120 mg P cm^{-3}, and (*high*) 3.89 mg N cm^{-3} and 0.190 mg P cm^{-3}

Results

Aboveground biomass and belowground biomass were linearly correlated ($R^2 = 0.91573$, $P = 0.0001$). Those variables therefore were summed to create total biomass per pot. Final total biomass varied significantly among salinity and nutrient treatments ($P = 0.0188$) (Table 2). Biomass in the highest nutrient concentration was not significantly different than the low (Louisiana state average) or medium nutrient treatments (Fig. 1). The lowest soil nutrient condition produced lower biomass than all other nutrient treatments except at the highest salinity (36 ppt), where biomass was low regardless of nutrients (Fig. 1).

Plant biomass ranged from 5 to 240.2 g ($n = 120$). When salinity was most stressful for *S. patens*, at 36 ppt, biomass remained low at 17.2 g pot^{-1} (ranged 11.2–23.2 g pot^{-1}) regardless of nutrient availability, but when salinity was least stressful for the plants, 6 and 2 ppt, biomass varied greatly with nutrient availability (Fig. 1). At 18 ppt, biomass averaged 31 g pot^{-1} (ranged 28.28–33.72 g pot^{-1})

in the lowest treatment, and 57.37 g pot^{-1} (ranged 51.19–63.55) in all other nutrient treatments. Low salinities with below average nutrients (lowest treatment) provided biomass 46.99 g pot^{-1} (ranged 41.75–52.23 g pot^{-1}) similar to the 18 ppt salinity lowest, low, and medium treatments. The highest average biomass of 142.5 g pot^{-1} (ranged 129.81–155.19 g pot^{-1}) occurred at low salinities of the medium nutrient treatment. We observed plants in the highest nutrient concentration displayed yellow leaves early in the experiment regardless of salinity, but regained normal color during the latter half of the experiment. Target salinities measured in both porewater and tub water were achieved and maintained as intended.

Discussion

Our results were consistent with the suggestion by Foret (2001) that salinity stress is primary to nutrient availability in limiting the growth of *S. patens*. Increasing nutrient availability did not enable plants to better tolerate salinity stress. At the highest target salinity (36 ppt), nutrient availability was irrelevant to total biomass, which averaged only 17.2 g pot^{-1}. The initial yellowing of plant leaves at all salinities in the highest nutrient treatment suggests overfertilization stressed plants early in the experiment and prevented plants from producing to their full potential biomass. At 18 ppt, total biomass did not differ among nutrient treatments that were at or above average nutrient availability (Fig. 1).

Only at the two lower salinity levels, did nutrient availability affect *S. patens* growth. At low salinity, the effect of nutrient availability on *S. patens* growth was considerable. Our study shows that the response of *S. patens* growth to nutrient availability varies with salinity such that nutrient availability has more effect on growth at lower salinity levels than at higher salinity levels. A theoretical relationship among plant growth, salinity, and nutrient availability based upon our data can be described graphically (Fig. 2).

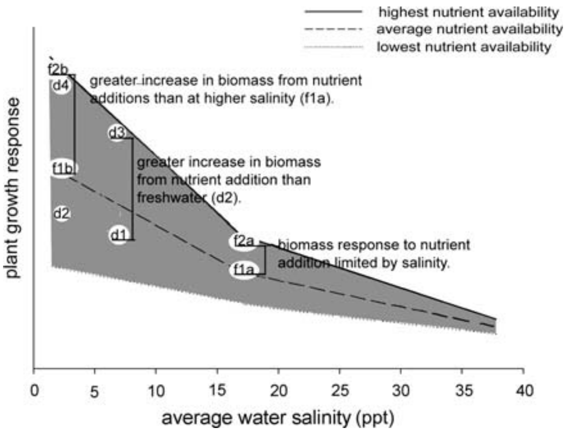

Fig. 2 Results of two previous studies illustrated on our proposed theoretical interaction of nutrient and salinity showing relationship of initial conditions in DeLaune et al. (2005) as *d1*, Foret (2001) as *f1a* for high salinity and Foret (2001) as *f1b* for low salinity relative to responses from salinity reduction (*d2*), nutrient addition (*d3*, *f2a*, and *f2b*) or both (*d4*)

The different conclusions reached by DeLaune et al. (2005) and Foret (2001) support and help illustrate the interaction we found. DeLaune et al. (2005) had lower initial salinity and perhaps lower nutrient availability than the field experiment used by Foret (2001). Ewing et al. (1995) reports *S. patens* does not decrease in biomass at 7 ppt, but signs of stress appear at 14 ppt. Salinity ranged between 6 and 8 ppt for DeLaune et al. (2005), which our data and those of La Peyre et al. (2001) suggest cause little stress for *S. patens*. Differences in nutrient availability could result from differences in soil bulk density (mass of soil per unit volume) alone. The site where DeLaune et al. (2005) collected the marsh soil-plant plugs is the same as site number 19 described in DeLaune et al. 2003 (personal communication, DeLaune RD). Soil bulk density there averaged 0.09 g cm^{-3} (DeLaune et al. 2003), whereas soil bulk density where Foret (2001) did his field experiment averaged 0.12 g cm^{-3}. Even if nutrient concentrations on a dry weight basis were similar in the Foret (2001) and DeLaune et al. (2005) studies, differences in bulk density would mean nutrient availability to plant roots was 33% greater in the Foret (2001) study than for DeLaune et al. (2005).

Considering the salinity tolerance of *S. patens*, effect of soil bulk density on nutrient availability, and the interaction of salinity and nutrients, the differing conclusions by Foret (2001) and DeLaune et al. (2005) support our proposed theoretical relationship between salinity and nutrient availability (Fig. 2). The initial conditions of their plants are represented on Fig. 2 by “d1” for “DeLaune 1”, “f1a” for Foret’s initial high salinity treatment, and “f1b” for Foret’s low salinity treatment. Plants used by DeLaune et al. (2005) likely experienced no salinity stress, and low nutrient availability initially (condition “d1” in Fig. 2). Moderately lowering salinity (from 8 to 0 ppt, from condition “d1” to “d2” in Fig. 2) caused an insignificant biomass increase. Substantially raising nutrient availability (10.0, 8.7, and 15.6 g N m^{-2}) without lowering salinity (from condition “d1” to “d3” in Fig. 2) caused a significant biomass increase. Making those changes in salinity and nutrient availability simultaneously (from condition “d1” to “d4” in Fig. 2) caused the greatest growth. Foret (2001) on the other hand, conducted his study with moderate nutrient availability and two salinities, 2–4 versus 13–24 ppt (conditions “f1a” and “f2b” on Fig. 2, respectively). Moderately increasing nutrient availability (36 g N m^{-2} $year^{-1}$, 2 g P m^{-2} $year^{-1}$) increased growth at low salinity (from condition “f1b” to “f2b” in Fig. 2) but not at high salinity (from condition “f1a” to “f1b”).

We did not vary soil aeration in our study. Soil was continually flooded, but anoxia stress was likely less than in nature because the high sand to clay ratio we used may have allowed more water movement and less oxygen demand than organic soils. Increases in sediment availability in the water column would likely alter soil anoxia by potentially increasing elevation and changing nutrient availability (Slocum et al. 2005). Additional studies of *S. patens* in which soil oxygen is varied with salinity and nutrient availability are needed. Anoxia and salinity reduce the efficiency of ammonium uptake in *S. alterniflora*, and other factors that control sulfide concentrations are thought to limit plant production irrespective of nutrient availability (Mendelssohn and Morris 2000).

Conclusion

We have demonstrated the importance of reducing salinity to allow benefits of nutrient uptake by *S. patens*, the most common emergent plant in Louisiana’s 16,000 km^2 coastal wetlands (Chabreck 1970). Restoration planners in Louisiana have selected against reintroduction projects that lack a significant sediment component, as demonstrated in the Louisiana Coastal Area Report (Army US Corps of Engineers (USACE) and Louisiana Department of Natural Resources (LDNR) 2004), and annual Coastal Wetland Planning Protection and Restoration Act priority project lists (http://www.lacoast.gov). While our study does not address a myriad of compounding complexities included in estuarine nutrient cycling, it indicates planners should consider the interaction of salinity and nutrient availability in both determining the placement of freshwater reintroductions and in estimating the effected area. Lane et al. (2004) concluded that freshwater reintroductions benefit only the area of outfall with increased production, because of the rapid uptake of nutrients in a fresh marsh. We hypothesis that the area of increased production (effected marsh area) resulting from a freshwater reintroduction into *S. patens* marshes also will include portions of the receiving area that are high salinity brackish marsh. However, the highest production potential would still occur in fresher areas where benign salinities allow greater nutrient uptake.

We showed that *S. patens* response to salinity depends partly on site-specific soil nutrient conditions. Although nutrient inputs to marshes from water reintroduction can be estimated during planning, ambient nutrient conditions in marshes also need consideration, because soil nutrient conditions vary across the coast (Brupbacher et al. 1973).

Sediment delivery is any method of getting soil material into a marsh from another location, for example pumping from a river bottom or spraying dredged material from bay bottoms. Restoration planners have considered using sediment delivery as a sole restoration technique or in combination with freshwater reintroductions with little information to determine which method to use (Army US Corps of Engineers (USACE) and Louisiana Department of Natural Resources (LDNR) 2004). Our results elucidate the complexities of such options; potential benefits from salinity reduction or nutrient addition depend on site conditions. Results of our study indicate that increasing nutrients alone in a *S. patens* marsh would not have a significant effect, except in fresh areas (<6 ppt). We propose salinity remain the primary concern in plans aimed at improving degraded *S. patens* marshes.

Acknowledgments We thank Rebecca Howard, Tom Minello, John Foret, Lawrence Rozas, Honora Buras and unknown reviewers for reviewing drafts of this manuscript. The Louisiana Department of Wildlife and Fisheries and UL Graduate Student Organization provided funding. Angela Burcham, Justin Price, and Regan Coussan provided indispensable data collection assistance. Analysis and writing were provided by the staff of

NOAA National Marine Fisheries Service and Louisiana State University.

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