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Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes

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Abstract

Salinity is a well-known stressor of *Phragmites australis* (common reed), leading to reduced success in brackish and salt marshes. Although saline, many remaining salt marshes in New England are changing in structure and function due to tidal restrictions and rapid proliferation of *P. australis*. The poor reputation of this native plant (its dominance is used as an indicator of marsh degradation) has stimulated management and research using natural stressors for control. Our field study associated natural variability in soil salinity levels over time and space with vigor and spread rates of *P. australis*. Over 2 years, salinity was measured 15 times from three depth intervals (5–20, 35–50, and 65–80 cm) at five stations established in six colonies of *P. australis*. Our results indicated that salinity in tidal marshes varied temporally due to the extent of tidal flooding (salinity was greater during spring tides compared with neap tides) and regional freshwater runoff (salinity was lower in the spring). If the growing season is split into early (May–July) and late (August–October) periods, interesting patterns emerged (salinity increased with depth early, but decreased with depth late). Shoot height, cover, and expansion rate of the six colonies were measured twice over 3 years. In general, the stands of *P. australis* were expanding into salt marsh at 0.35 m per year, and increasing in cover (8% per year), even though the canopy height decreased at all but two of the sites over the study period. Salinity was lower in marshes where tides were artificially restricted (11–16 ppt compared with 19–24 ppt for the natural marshes), and one of these sites exhibited rapid *P. australis* expansion. At sites with natural hydrology, *P. australis* appeared to be expanding more slowly, shading out marsh species, and perhaps avoiding salinity stress by accessing natural sources of fresher water at different soil depths during different seasons. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Invasive species; New England; *Phragmites*; Population expansion; Salinity; *Spartina*; Tidal restriction

1. Introduction

Salinity is a well-known stressor of *Phragmites australis* (Cav.) Trin. Ex Steudel (common reed). Although widely distributed in shallow freshwater marshes across North America and Europe, *P. australis* distribution in tidal marshes appears to be limited by salinity (Chambers et al., 1999). Descriptive observations along salinity gradients show reduced vigor and success in brackish and salt marshes (Gallagher et al., 1987; Hanganu et

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al., 1999). Experimental evidence clearly indicates salinity is an important stressor for *P. australis* (Hellings and Gallagher, 1992; Lissner et al., 1999), though different varieties cope with varying degrees of success in natural settings (Hauber et al., 1991; Hanganu et al., 1999). In 1994, Burdick and Dionne suggested *P. australis* may obtain fresher water at depth, and ground water flow has been shown to support stands where surface water salinity is too great (Lissner and Schierup, 1997). Recently, Adams and Bate (1999) have shown natural stands of *P. australis* in mesohaline estuaries of South Africa occur at sites of ground water input. Their experimental work emphasized the point Lissner and Schierup made in 1997, *P. australis* distribution and success depends upon the salinity of interstitial soil water, not surface water.

Although saline, many remaining coastal marshes in New England are being invaded by expanding populations of *P. australis* (Chambers et al., 1999). This may be due to soil disturbance, altered hydrology, or genetic changes in the species (either through introduction of new varieties, hybridization of varieties, natural evolution, or a combination of such process). Spoil banks associated with ditching and filling marshes (especially along roads) disturbs the soil; and bare, oxidized soil provides an appropriate site for colonization by seed (Haslam, 1971; Witje and Gallagher, 1996). Hydrologic alterations are perhaps the major factor leading to invasion of natural marshes by pre-existing stands of *P. australis*. Alterations to the natural hydrology of salt marshes include, (1) tidal restrictions that lower flood frequency as well as salinity (Roman et al., 1984; Burdick et al., 1997); and (2) increasing fresh water discharge in channels, over the soil surface, and through ground water. Tied with hydrologic alterations are levels of nutrients and toxins, notably nitrogen and sulfides, respectively. Access to greater nutrient concentrations and exposure to lower sulfide levels in groundwater also could promote expansion of *P. australis*. For example, nitrogen (as proline and other compounds) is widely utilized by marsh plants to balance osmotic stress (Briens and Larher, 1982). On a larger scale, it is possible that greater atmospheric inputs of nitrogen and greater carbon dioxide levels (Jaworski et al., 1997) could be altering the competitive balance that would favor *P. australis* (C3 fixation path) over *Spartina* species (C4 path).

Tidal restrictions not only prevent tides from conducting salt water into and fresh water out of the marsh, they often lead to subsidence through oxidation of marsh peat that lowers the sediment elevation (Burdick et al., 1997; Portnoy and Giblin, 1997). Subsidence increases slopes and ground water flow entering the marsh edges at or near the surface. The creation of vertical barriers (and filling behind them) at marsh/upland edges is a popular method of protecting human property that is subject to coastal flooding and erosion. This practice prevents tidal flooding and by effectively steepening the banks, causes the groundwater level to rise landward of the marsh. The result is an increase in surface and shallow ground water flow entering the edge of the marsh at the ground surface, supplying *P. australis* with fresher water than would normally be available. Further, it prevents marsh expansion into upland, which occurs naturally with rising sea levels (Redfield, 1972). Both subsidence and filling can increase fresh water flow into marsh edges.

P. australis is more likely to be found at sites of surface ground water discharge and appears to access deeper, less saline water (Adams and Bate, 1999). However, *P. australis* has been found to grow successfully where soil salinity is greater than 20 ppt (Burdick and Dionne, 1994; Chambers, 1997). At these sites, *P. australis* may have mechanisms that reduce its exposure to levels of salinity that would produce stress and reduce success. Often soil salinity measurements are limited to mid-summer, after anthesis, and too late for salinity stress to impact plant height (vigor) or sexual reproduction. From May to July, the period of ecological importance to *P. australis* in terms of competition for light and reproduction, few data are available. Yet this may be the critical time to determine soil salinity and the effects of salinity stress on *P. australis*. Could *P. australis* use low soil salinity in spring to expand into high marsh at the expense of *S. patens*? In New England, snow melt and spring rains can reduce estuarine salinity to very low levels during the phase of rapid growth (May–July). We wished to determine whether invading stands of *P. australis* could escape salinity stress by exploiting spatial and temporal patterns in interstitial soil salinity. Stand characteristics and the spatial and temporal patterns of soil salinity were examined in six stands of *P. australis* that appeared to be invading natural and tidally restricted salt marsh to test two sets of hypotheses (presented as H_a).

Set A. Salinity varies spatially and temporally in salt marshes.

1. Salinity increases from the center of *P. australis* stands toward *Spartina* stands.
2. Deeper wells have lower salinity than shallow wells.
3. Lower salinity is found in the spring and early summer (due to snowmelt and spring rains).
4. Salinity should be relatively greater during periods of spring tides when tides are highest.

Set B. *P. australis* patches are supported by fresh water flowing from surrounding uplands and occur at sites where salinity is relatively low.

1. Upland edges of marshes with *P. australis* stands have lower salinity than adjacent edges without *P. australis*.
2. Cover and stature of *P. australis* decrease (as salinity increases) from upland edge to marsh creek.
3. Stands of *P. australis* are expanding into salt marshes.
4. Among the six different stands, greater expansion rates are associated with lower soil salinity.

2. Materials and methods

2.1. Sampling sites

Seven stands of *P. australis* were chosen as study sites in or near the Rough Meadows Wildlife Sanctuary in the Great Marsh, Rowley, Massachusetts (Fig. 1). One stand was mowed by tractor and subsequently dropped from the study. Two stands were located upstream of undersized culverts that restricted tidal flooding, Mud Creek and Railroad sites. Although culvert size was increased at the Railroad site during the study, the site is still considered tidally restricted. Other sites occurred in areas with no hydrologic alterations, Oak Knoll # 1; Oak Knoll # 2; Far Road # 1; Far Road # 2. Stands often occurred in marsh ‘pockets’, i.e. indentations in the upland, where dense *P. australis* graded into marsh dominated by *Spartina patens*. To minimize issues of genetic differences and disturbance, we selected stands in apparently undisturbed marsh within a circle of 1 km radius.

2.2. Sampling design

At each site, five stations were established for the collection of plant and salinity data, a three station transect and two additional stations (Fig. 2). For the transect, station 1 was at the center of a *P. australis* stand; station 2 was located in the center of the transition zone (*P. australis* grading into *S. patens*); and station 3 was placed in *S. patens*, mid-way between station 2 (transition) and the nearest tidal creek. Station 4, also in the transition zone but laterally offset from the transect, provided another site similar to station 2, to determine the variability within the transition zone. The final station, station 5, was established at each site an identical distance from the upland to the transition zone (as in stations 2 and 4), but where *P. australis* was not present. These stations were established to yield information on small-scale variability regarding different salinity conditions, and on the likelihood of invasion by *P. australis* laterally along the marsh.

2.3. Salinity measurements

Arrays of wells were established at all five stations to collect interstitial soil salinity, including the three stations along the transect (horizontal profile). Each array consisted of three wells that covered three different depths, 5–20; 35–50; and 65–80 cm. Salinity wells were constructed from plastic pipe, 1.6 cm inner diameter and drilled with two opposing 3 mm holes every 5 cm over the sampling depth. The base of each pipe was sealed with tape, and the top was fitted with a reducing couple and two 90° angle joints so that rainwater as well as flooding tidewater were prevented from entering the pipe. Water was removed from the wells by tubing attached to a plastic 50 ml syringe and measured with a temperature corrected optical refractometer (± 1 ppt). Wells were sampled at low tide during the growing season (six occasions between July and October in 1996 and nine occasions between May and October in 1997). The growing season from April 20 to October 20, was split evenly at July 20 to define early and late periods. Sampled dates included both spring and neap tide periods.

2.4. Plant measurements

Characteristics of *P. australis* (percentage of cover and canopy height) and the position of the transition zone were measured in the fall of 1996, 1998 and 1999. Plant cover was assessed on either side of the stations using a hoop 1 m^2 in area. All vascular species were identified and enumerated to the nearest 5% cover (nearest 1% if under 5%) based on 100% maximum cover. Canopy height to the nearest cm was estimated for *P. australis* and *S. patens* as the height that was exceeded by 20% of the mature shoots. The transition zone was defined as the distance along a transect where *P. australis* composed less than 95% (inner edge) but greater than 5% (outer edge) of the total plant cover. Distances from the well array (station 2) to the inner and outer edges of the transition zone were determined. Expansion rates were calculated for both periods and edges and these values were

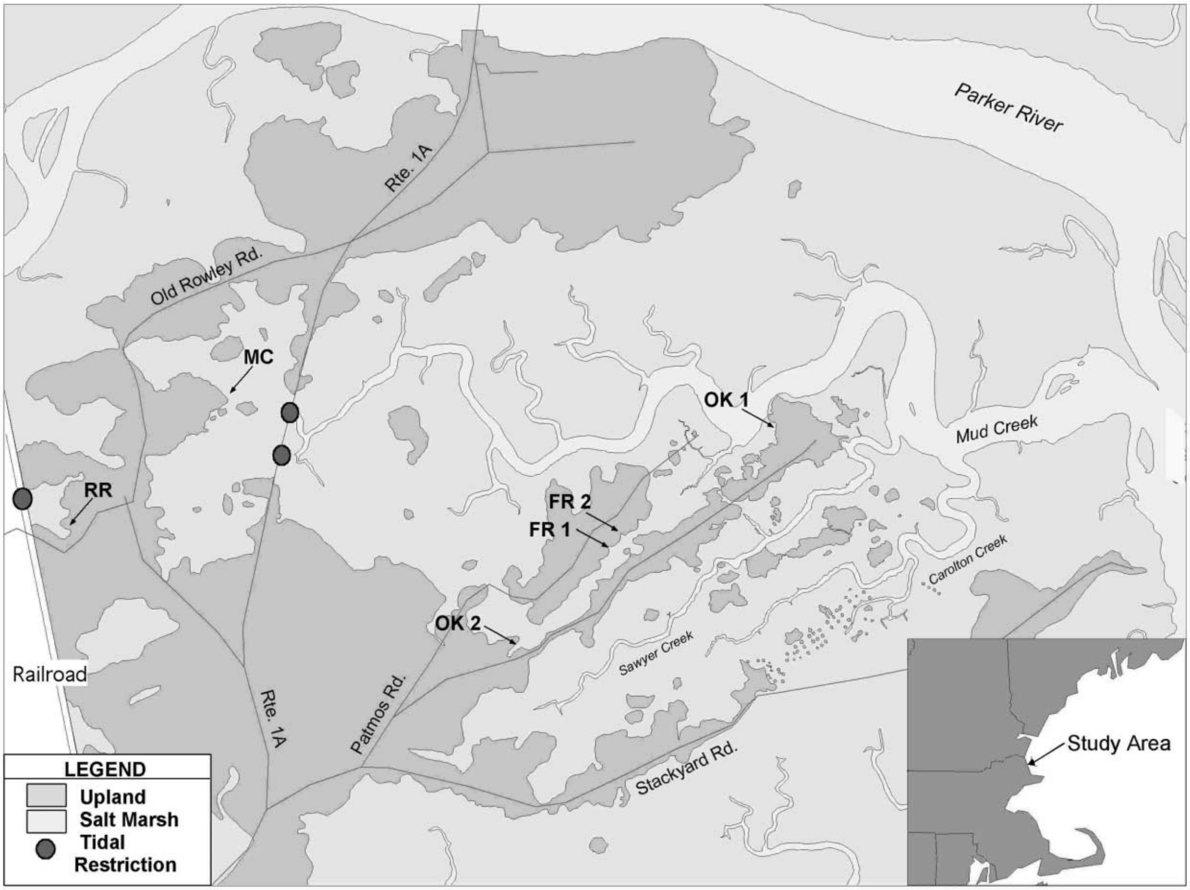

Fig. 1. Location of the Great Marsh along the north shore of Massachusetts, USA, and the six study sites, RR, Railroad; MC, Mud Creek; OK1, Oak Knoll # 1; OK2, Oak Knoll # 2; FR1, Far Road # 1; and FR2, Far Road # 2.

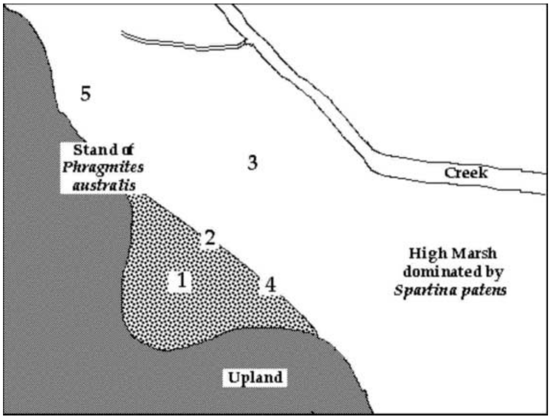

Fig. 2. Placement of sample stations within a typical stand of *P. australis* that is invading a salt marsh dominated by *S. patens*. Stations 1–3 form a transect from the center of the stand to the transition zone to the area dominated by *S. patens*. Station 4 is in the transition zone offset from the transect and station 5 is in an area without *P. australis*.

averaged to yield an average annual rate of expansion for each stand.

2.5. Statistics

Analyses of variance (ANOVA) were run on the salinity data using site, station and depth as main effects with two-way interactions. Additional analyses were run with the dates split into early and late growing periods and with the dates split into spring and neap tide periods. To avoid issues regarding repeated measures, data were averaged for all collections or each period examined (e.g. spring vs. neap tides) to test for differences between periods. Differences among means were tested post hoc with alpha set at 0.05 using Fischer's protected *F*-test except when comparing means with unequal *n*, in these cases Tukey's modified HSD was used (SuperANOVA, Abacus Concepts, 1989). Plant stand characteristics measured in 1998 and 1999 were analyzed using ANOVA with station as the main effect. Student's *t*-tests were used to determine significance of change rates for the six stands following Lamda Wilks tests for normality using JMP software (SAS Institute Inc., 1995). Spearman and Pearson correlations were used to examine relationships between soil salinity and plant stand characteristics.

3. Results

3.1. Salinity

Salinity patterns are explained by three ANOVA models of increasing complexity.

Model one. Interstitial soil salinity collected from wells in six stands of *P. australis* grading into *Spartina* were averaged over all dates, and the 90 means were analyzed using ANOVA with fixed effects (Table 1). The model explained 94.5% of the variability in salinity. Site had the largest effect on soil salinity, followed by station and depth. The two hydrologically restricted sites had the lowest salinities (11 and 16 ppt) with the four natural sites averaging 19–24 ppt (Fig. 3).

In general, station 1 in the center of the *P. australis* stands had the lowest salinity, and station 5 where *P. australis* was absent, had the greatest (Fig. 3). There was no significant difference between salinity at stations 1 and 3. Therefore, the gradient we expected to find from station 1–3 was not evident when all dates were averaged. This result indicates we should accept the null hypothesis associated with set A 1, salinity did not increase from *P. australis* stand to *Spartina* marsh, but we only do so provisionally (see model three). Interestingly, station 4, which was established as a replicate of station 2, was significantly more saline than station 2, but similar to station 5 (accept Ha, set B #1, salinity at station 2 < 5, but modify to accommodate result of salinity at station 2 < 4). Also, shallow wells sampling 5–20 cm depth soils were the most saline (accept Ha, set A #2). Some interactive effects were significant, and these will be examined in the more complex models.

Model two. The data was examined using season (early/late) and tide (spring/neap) as main effects in addition to site, station and depth (Table 1). Salinity samples were collected five times (three spring and two neap periods) during the early period, and ten times (five spring and five neap periods) during the late period of the

Table 1
Results from ANOVA (type III sums of squares) of soil salinity collected from wells in six stands of *P. australis*

	Total	Main effects					Interactions					
		Site	Station	Depth	Season	Tide	Site × station	Site × depth	Station × depth	Site × season	Season × depth	Site × tide
Model one												
R^2/df	0.945/90	5	4	2			20	10	8			
F ratio	14.2	99.1	11.2	6.5			5.3	2.6	1.1			
P value	0.0001	0.0001	0.0001	0.036			0.0001	0.016	0.410			
Model two												
R^2/df	0.845/356	5	4	2	1	1	20	10		5	2	
F ratio	33.4	110	22.5	1.5	443	63.8	7.8	2.8		4.5	16.1	
P value	0.0001	0.0001	0.0001	0.221	0.0001	0.0001	0.0001	0.0026		0.0006	0.0001	
Model three A (only early data)												
R^2/df	0.866/176	5	4	2		1	20	10	8			5
F ratio	14.1	69.2	31.1	5.3		7.3	10.2	2.7	2.8			2.7
P value	0.0001	0.0001	0.0001	0.0064		0.0079	0.0001	0.0055	0.0072			0.0240
Model three B (only late data)												
R^2/df	0.902/180	5	4	2		1	20	10	8			5
F ratio	20.8	142	12.4	28.6		128	6.7	3.7	2.5			2.0
P value	0.0001	0.0001	0.0001	0.0001		0.0001	0.0001	0.0002	0.0142			0.0811

growing season. Soil salinity varied seasonally, with fresher soil water found in the early period (spring and early summer) and higher salinity in the late period (accept Ha set A, # 3; Fig. 4). The lunar period was less important than season in explaining salinity variation, but was significant (Table 1), with spring tides associated with greater salinity (accept Ha set A, # 4; Fig. 4). Averaged over all sites, salinity increased from deep to shallow wells as we hypothesized, but the season by depth interaction indicated this pattern was present only during the late period (Fig. 4). Surprisingly, the opposite trend was true for the early period, which was less saline overall. Thus, both Ho and Ha set A, # 2 must be rejected; and an alternative hypothesis may be proposed to account for these results.

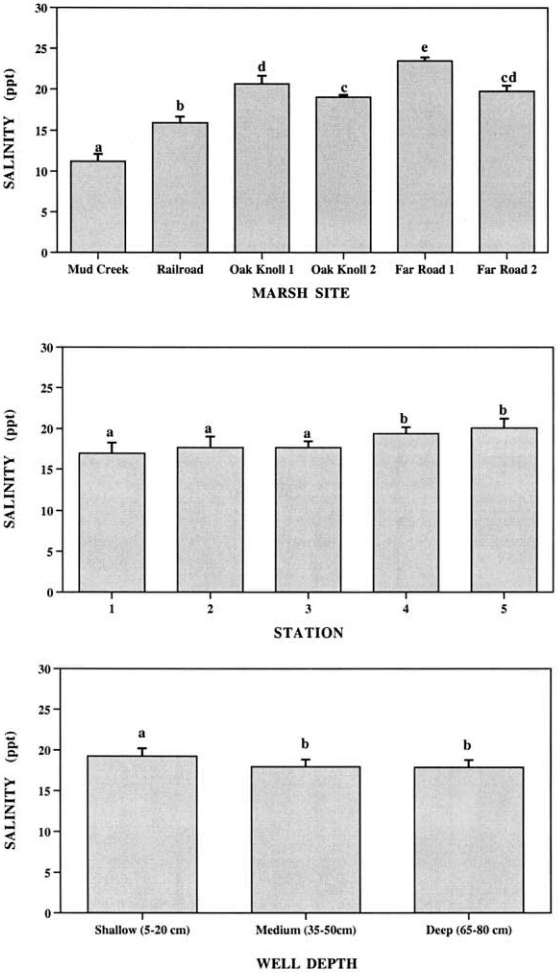

Fig. 3. Soil water salinities collected from wells averaged according to the main effects in model one, site; station and depth. Different letters above S.E. bars indicate significant differences between means.

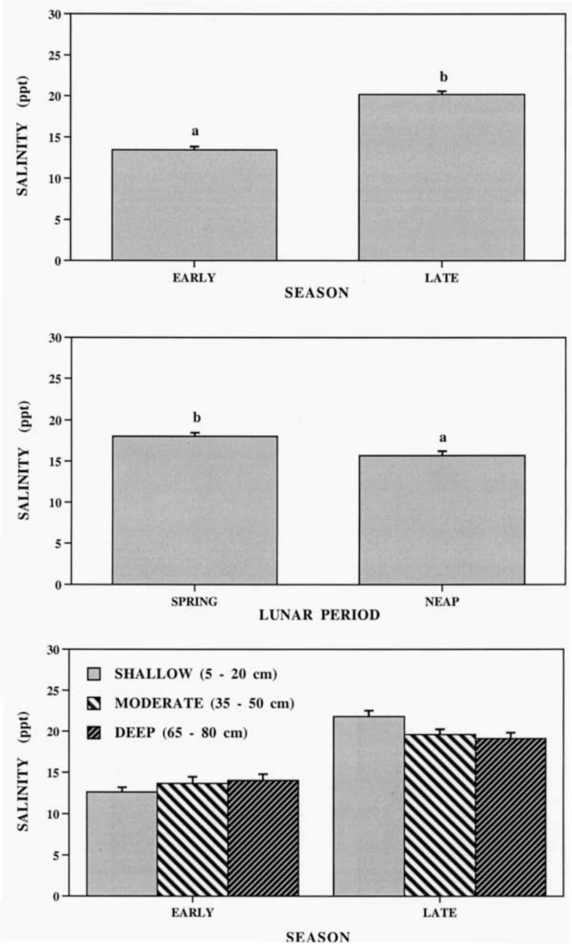

Fig. 4. Soil water salinities collected from wells averaged according to the additional main effects of season and lunar period in model two, as well as season by depth interaction. Different letters above S.E. bars indicate significant differences between means.

Model three. Since the early period may be critical to the competitive interactions that allow *P. australis* expansion in *Spartina* marshes, we have examined the data using our main effects of site, station, depth, and tide for samples collected only during the early period in model three A, and only during the late period in our model three B ANOVA. Model three A explained 86% of the variability in the 176 salinity means. Site, station and their interaction accounted for most of this variability (Table 1). Only one tidally restricted site stood apart, with the lowest average soil salinity in the early period (6.9 ppt). This contrasts with the late period analysis which shows the two restricted sites much less saline than the areas with natural hydrology (Fig. 5). During this period, water of less than 20 ppt salinity was only available at the two hydrologically restricted sites. There was a clear trend from lower to higher salinity (10.0–13.5 ppt) along transects from *P. australis* stands to *Spartina* marsh, but only early in the growing season (Fig. 5). Therefore, Ha set A # 1 can be accepted if it is amended to specify the early period.

> Ha. Salinity increases from *P. australis* stands to *Spartina* stands during the early part of the growing season.

There was a significant interaction between site and station ($P < 0.001$) for both early and late periods, but no trends were evident other than those due to hydrologic restriction (Fig. 6). Specifically, when the two tidally-restricted sites were coupled to compare them with marsh areas having natural hydrology, significantly lower salinities were found in the restricted marshes ($P < 0.0001$). The interaction of site by depth was also significant. The trend of increasing salinity with well depth was surprisingly absent for the two tidally restricted sites during the early period (Fig. 6). Although shallow wells showed little difference across the transect from station 1 to 3, deep wells averaged 8.1 ppt at station 1, climbing to 14.3 ppt at station 3 during the early period (Fig. 6). However, during the late period, average salinities in deep wells remained under 20 ppt across the transect, while shallow wells increased in salinity from 19 to 22.6 ppt from station 1 to 3 (Fig. 6).

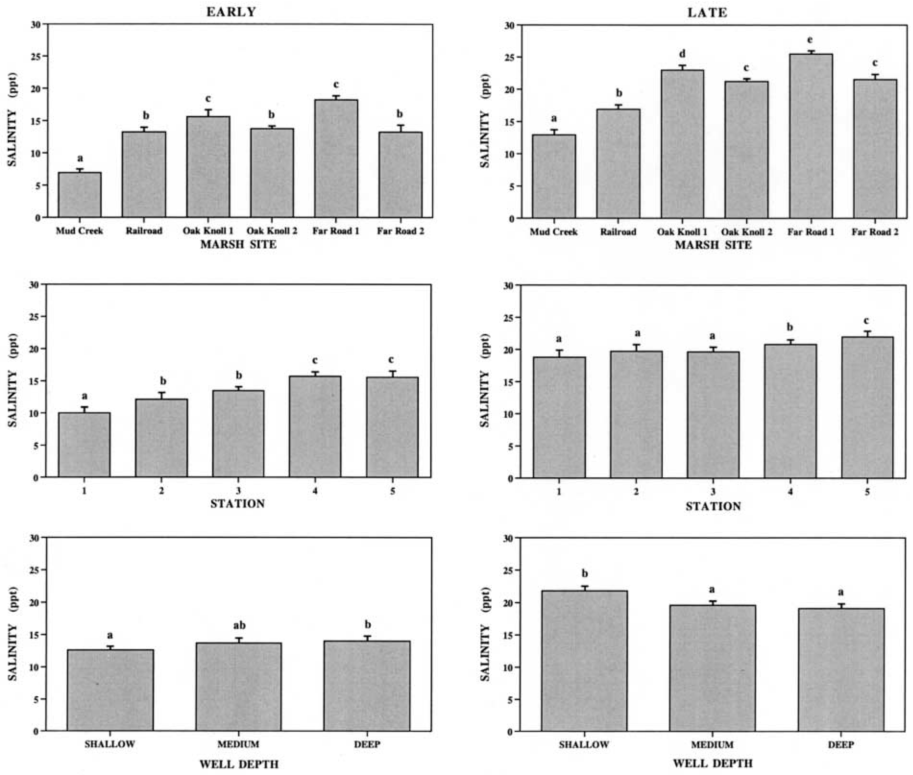

Fig. 5. Soil water salinities collected from wells averaged according to the main effects of site, station and depth in model three for both seasonal periods, early and late. Different letters above S.E. bars indicate significant differences between means.

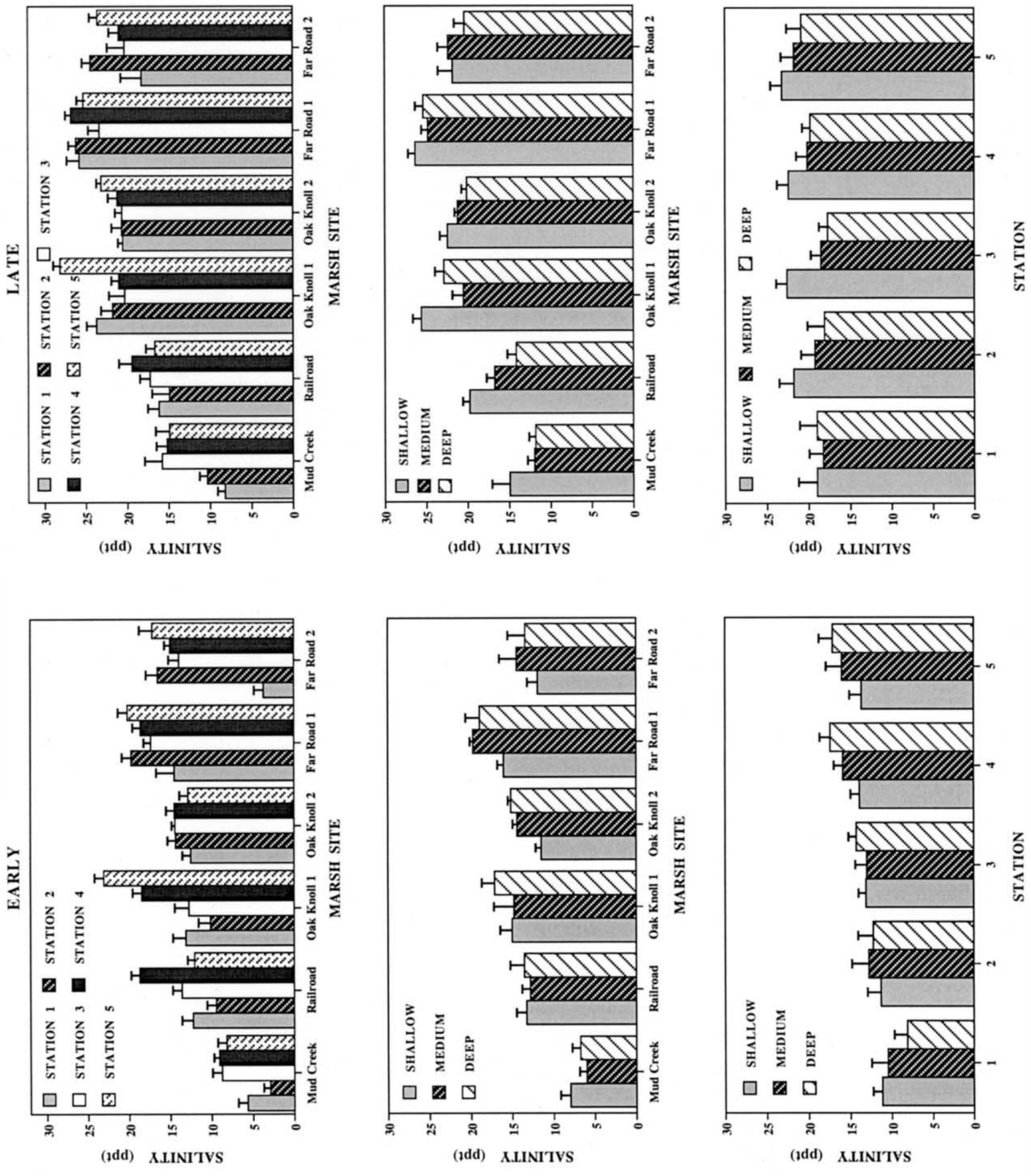
EARLY
LATE
STATION 1
STATION 2
STATION 3
STATION 4
STATION 5
SHALLOW
MEDIUM
DEEP
SALINITY (ppt)
0
5
10
15
20
25
30
Mud Creek
Railroad
Oak Knoll 1
Oak Knoll 2
Far Road 1
Far Road 2
MARSH SITE
1
2
3
4
5
STATION

Fig. 6.

3.2. Plant stands

Canopy height and cover of *P. australis* were generally greatest at station 1, located near the center of all six stands. Both height and cover were significantly less at the transition area, station 2 (repeated measures analysis; accept Ha set B #2; Table 2). From 1996 to 1999, cover increased at all the *P. australis* stands (stations 1, 2 and 4; $P < 0.01$), with strongest increases at the two restricted sites, as well as Far Road #1 (Table 2). Canopy height showed a different pattern, with no significant change over all sites. Instead, canopy height increased only in Mud Creek (restricted hydrology) and Far Road #2 (natural hydrology). The restricted Railroad site and the other three sites with natural tidal hydrology showed large average annual declines in stature (Table 2).

P. australis stands measured at station 2 (averaged over 3 years and averaged for inner and outer transition zones) were expanding over the study period at a rate of 0.34 m per year ($P < 0.05$; accept Ha set B #3). The expansion rate was greatest at Mud Creek, followed by Far Road #2 (Table 2). These sites were the only two that had average annual increases in both the cover and canopy height. Expansion rates of *P. australis* at the six sites were positively correlated with changes in plant height (Table 3). Oak Knoll #1 was the only site where *P. australis* retreated. Intermediate rates of expansion were found at the other two sites having natural hydrology, averaging about 0.3 m per year over the 3 years. The slowest positive expansion was observed at Railroad, the site where a culvert that restricted tides was replaced with a larger culvert (35 increased to 45 cm in diameter) in fall 1996. This action likely increased tidal flow and consequently salinity, leading to loss of canopy height and a lower expansion rate.

With the limited number of stands examined and the change in hydrology at the Railroad site during the study, the effect of restricted tidal hydrology on expansion rate was not significant, nor was the effect of average salinity level (accept Ho set B #4). The expansion rate of the stands was negatively correlated with average salinity levels at both stations 1 and 2 (Table 3), but these associations were not significant. The change in canopy height and cover of *P. australis* at station 2 were both negatively correlated with salinity at stations 1 and 2. However, these correlations were only significant between salinity at station 1 and change in canopy height at station 2 (Table 3).

4. Discussion

The spatial variability we found in soil salinity supports the idea that *P. australis* is taking advantage of estuarine marsh areas with reduced salinity. Conclusions regarding variability in soil salinity over space and time were somewhat dependent upon the complexity of the model used. In the spring, runoff from rains and snowmelt freshen surface soils, but surface soils become more saline than deeper soils in the latter half of the growing season (Fig. 6). Although we cannot rule out potential access to fresher water at depths greater than 80 cm, Lissner and Schierup (1997) reported that maximum root depths of *P. australis* in six saline habitats ranged from 40 to 85 cm.

Adams and Bate (1999) report salinity was fresher in soils than in waters flooding estuarine stands of *P. australis*, stressing the importance of ground water seeps in maintaining these coastal populations. The patterns we found in soil salinity (station 1 < 2 and 3; station 2 < 5) also indicate *P. australis* occurs in marsh areas influenced by ground water. Lissner and Schierup (1997) found that soil water salinity generally decreased with depth in the rooting zone of saline coastal stands of *P. australis*, and in most cases did not reflect the salinity of the flooding surface water. However, the trend was inconsistent, and depended upon sampling date, especially in the upper por-

Fig. 6. Soil water salinities collected from wells averaged according to the interactive effects of site by station, site by depth, and station by depth in model three for both seasonal periods, early and late. Bars are S.E. of the means.

Table 2
Plant characteristics and soil salinity (averaged over all dates and depths) of six stands of *Phragmites* invading *Spartina* salt marsh

Site station	Hydrology	Salinity (ppt)	Cover in 1996	Canopy HT in 1996 (cm)	Cover change 96–99 (% per year)	Canopy HT change 96–99 (cm per year)	Expansion rate (m per year)
Mud Creek	Restricted						
1		7.1	18	163	+10.8	+1.0	
2		8.7	13	104	+18.3	+19.0	+0.94
4		13.5	38	126	+4.0	+0.8	
Railroad	Restricted						
1		15.4	70	216	+6.7	−13.3	
2		13.4	43	170	+8.2	−20.0	+0.19
4		19.4	20	143	+16.7	0.0	
Oak Knoll 1	Natural						
1		21.2	90	203	−1.7	−21.0	
2		17.9	20	168	+3.3	−27.0	−0.10
4		20.1	19	139	+10.3	−7.0	
Oak Knoll 2	Natural						
1		18.5	70	175	−3.3	−18.3	
2		19.0	48	175	+5.0	−11.3	+0.32
4		19.3	28	175	+13.2	−9.8	
Far Road 1	Natural						
1		23.3	40	228	+17.5	−21.7	
2		24.4	14	191	+8.7	−29.3	+0.30
4		24.5	5	153	+18.3	0.0	
Far Road 2	Natural						
1		16.3	85	192	0.0	+3.3	
2		22.5	45	147	+6.0	+5.3	+0.41
4		19.6	38	166	−1.8	+3.0	

tion of the rooting zone. They found die-back occurred at the outer saline fringe of sites where salinity of deeper soils remained over 20 ppt. Presumably, previous expansion of the stands occurred when soil salinities were lower prior to their sampling period (July–October). Our results demonstrate much lower salinity earlier in the growing season (no stations within *P. australis* stands averaged over 20 ppt) with deep wells the most saline under natural hydrologic conditions (Figs. 5 and 6). However, the trend with depth switched later in the growing season when shallow wells were the most saline and averaged over 20 ppt (Figs. 4 and 5). We found that no low salinity water is consistently available to the entire *P. australis* stand over the entire growing season.

Due to its clonal habit, *P. australis* is not limited to capturing water of lower salinity at the site where it roots. Through its rhizome network, *P. australis* may be physiologically integrated with connected culms that have access to less saline water, but this idea was rejected by Lissner and Schierup in 1997. Functional connections have been demonstrated in other salt marsh plants, including *S. patens* (Hester et al., 1994), and earlier workers had suggested physiological integration controls stand characteristics in *P. australis* (Hara et al., 1993). More work is needed to determine whether *P. australis* may escape salinity stress by capturing lower salinity water through its clone network.

Between 1996 and 1999, *P. australis* expanded at five of our six study sites, with the greatest expansion at the freshest site that was also tidally restricted. At the Railroad site, the average expansion rate was low, even though soil salinity was fresher than at the unrestricted sites. Possibly, the larger culverts installed in 1997 led to greater tidal hydrology and a negative plant response. In a related study of a marsh restoration project ca. 20 km to the south, the point intercept method was used to measure expansion and retreat of *P. australis* stands along eight transects. *P. australis* expansion averaged 1.0 m per year along seven transects prior to restoration, but then retreated at a rate of 3.8 m per year for 2 years after tidal restoration (R. Buchsbaum, unpublished results). At Sandy Point, Great Bay National Estuarine Research Reserve (30 km north of the Great Marsh), a ditch (50 × 50 cm) was excavated in a salt marsh parallel to the upland through an advancing monoculture stand of *P. australis*. The ditch halted the advance of *P. australis* and increased plant diversity within existing stands. However, it was unclear whether drainage of fresh water, increased saltwater flooding, or physiological isolation of the seaward portion of the stand was most important in controlling *P. australis* (Burdick et al. 1999).

Several researchers in the United States have found associations between salinity levels and expansion rates in oligohaline and mesohaline tidal

Table 3
Correlation matrix of average salinity and plant characteristics in the transition zone (station 2) of six stands of *Phragmites* invading *Spartina* salt marsh

Station variable	Salinity (ppt)		Change in	
	Station 1	Station 2	Cover	Can. Ht.
Station 1				
Cover change 96–99 (% per year)	+0.07	+0.07		
Canopy height change 96–99 (cm per year)	−0.98	−0.37		
Station 2				
Cover change 96–99 (% per year)	−0.44	−0.60		
Canopy height change 96–99 (cm per year)	−0.90	−0.53	+0.65	
Expansion rate (m per year)	−0.69	−0.43	+0.89	+0.86

Values reported are Pearson correlations. Underlined values are significant at $\alpha = 0.05$ for both Pearson and Spearman (rank) correlations.

marshes (review in Chambers et al., 1999; Rice et al., 2000), but fewer data exist for polyhaline marshes (> 18 ppt). Havens et al. (1997) reported *P. australis* was invading constructed wetlands in Virginia. In six polyhaline marshes, they found that stands occupied 1–14% of the marsh area, demonstrating that *P. australis* can effectively colonize disturbed sediments and expand even in constructed polyhaline salt marshes.

In the Great Marsh, expansion of *P. australis* was statistically significant, but expansion rates were not significantly correlated with salinity. Canopy height, an indicator of vigor, declined over time at all but the two most-rapidly-expanding stands. The decline in canopy height was accompanied by increases in cover of *P. australis*. This may be an indicator of salinity stress, as indicated by Hanganu et al. (1999) who suggest declining shoot height associated with an increase in the number of shoots as an indicator of salinity stress.

In our study, *P. australis* expanded out from upland edges of marshes into high marsh dominated by *S. patens*. This is distinct from other studies in which *P. australis* expanded into low marshes dominated by *Spartina alterniflora*. In 1997, Chambers reported that sulfide, not salinity, was important in limiting distribution of *P. australis* in low marsh at the mouth of the Housatonic River, Connecticut. Later work suggested tidal restrictions allow rapid *P. australis* expansion by improving soil conditions in terms of sulfides and nutrients (Chambers et al., 1998). While we believe salinity is a significant factor limiting *P. australis* expansion at our site, we do not discount the potential stresses imposed by elevated sulfide or low nutrient levels. The fresh water flow from the adjacent uplands that appears to support *P. australis* through lowering salinity likely also improves soil conditions with respect to sulfide concentrations and may supply greater nitrogen to aid in osmoregulation.

Greater height and rooting depth of *P. australis* compared with *S. patens* and *S. alterniflora* allows *P. australis* to capture light and lower salinity water more effectively than its competitors (Fig. 7). Even though *P. australis* is not physiologically adapted to thrive in salt marshes, it can escape salinity stress and shade out *Spartina* spp. competitors. Our results are consistent with a model that shows *P. australis* can invade salt marsh where an upland ground water source flows into the marsh (Fig. 7). Field experiments manipulating water movement from surrounding uplands would provide an interesting test of this model. Furthermore, improvements in our understanding of how salinity stresses *P. australis* are needed to manage this species, which continues to increase its dominance in brackish and salt marshes in the US.

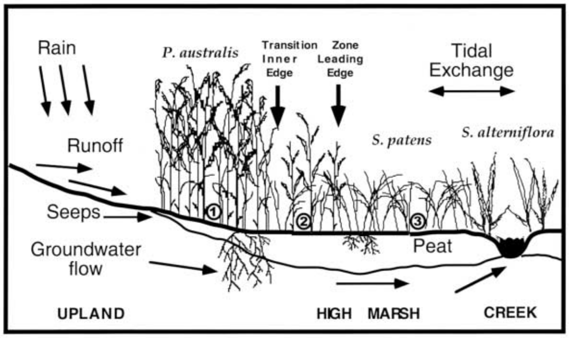

Fig. 7. Factors affecting soil salinity and expansion of *P. australis* in salt marshes. Numbers reflect relative positions of the sample well arrays (# 1– # 3) along the upland to creek transect.

We conclude *P. australis* invasion of salt marshes (in addition to brackish and fresh tidal marshes) is an important concern for coastal managers. Human alteration of salt marshes can enhance conditions favorable for *P. australis* expansion through restriction of tides that, (1) reduce fresh water drainage from the marsh; (2) reduce salt water flooding of the marsh; and (3) reduce vertical accretion and increase subsidence of the marsh surface leading to greater slopes and seep activity at marsh edges. Under natural tidal hydrology, soil salinity in stands of *P. australis* was greater than under restricted tides (Mud Creek and Railroad sites). This was especially true late in the season, when salinity at stations 1 and 2 averaged less than 15 ppt at the two restricted sites and 20–26 ppt at the four unrestricted sites. At both restricted sites, soil salinity at station 5 was low, indicating the opportunity exists for rapid lateral expansion of *P. australis* along the upland border. Expansion of existing stands in the high marsh adjacent to upland is likely to be accelerated by tidal restrictions and slowed by increasing tidal exchange.

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