Fertilization Favors Grasses Over Forbs

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Research Article

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Abstract

There are forb-dominated communities unique to salt marshes of the northernmost Atlantic states of the USA, the New Brunswick coast of the Bay of Fundy and the St. Lawrence Estuary that are not associated with exceptionally high soil salinity or saturation. These forb-dominated (predominantly *Plantago maritima* and *Triglochin maritima*) and *Spartina patens*-dominated communities were subjected to monthly fertilization with a slow-release nitrogen fertilizer in a Bay of Fundy marsh. After 20 years forb cover significantly declined where they had been dominant and are being replaced by grasses (predominantly *S. patens* and *Spartina alterniflora*). This shift is likely due to the increased availability of nitrogen which conferred a competitive advantage to *S. patens* and *S. alterniflora*. These grasses require nitrogen for production of osmolytes, chemicals which reduce osmotic stress due to saline soils. In contrast, *Plantago maritima* and *T. maritima* do not depend upon nitrogen for their osmolyte production. In marshes to the south forb communities are only associated with exceptionally high soil salinity or saturation. Results of our experiment suggest that absence of forb communities similar to those of higher latitudes could be due to historically greater availability of nitrogen in marshes to the south.

Introduction

In Northwest Atlantic tidal salt marshes graminoids are recognized as the dominant species (Wigand and Roman 2012, Baldwin et al. 2012, Pennings et al. 2012). Although forbs are common, they are usually reported to occur in low abundance. Widely recognized exceptions are when they are dominant in communities associated with high soil salinity or highly, permanently saturated soils (e.g., Ewanchuk, & Bertness 2004). However, on the coasts of the northernmost Atlantic states of the USA, the New Brunswick coast of the Bay of Fundy (Chmura et al. 1997) and the St. Lawrence Estuary (Létourneau 1996) communities dominated by the forbs *Plantago maritima* and *Triglochin maritima* occur outside of those extreme conditions. Controls on the occurrence of those forb communities have been suggested (Chmura et al. 1997), but little studied.

The controls on occurrence of graminoids in salt marshes of the Northwest Atlantic have been studied, particularly the role of nutrient availability in competitive success of grasses. On the coast of the Northeast USA Levine et al. (1998) reported that experimental fertilization shifted dominance from *Spartina patens* (= *Sporobolus pumilus*) to *Spartina alterniflora* (= *Sporobolus alterniflorus*) – the two species that comprise most of the vegetation cover there (Wigand and Roman 2012). To date, we have not found published studies of the impact of nutrient enrichment on forb-dominated communities.

Here we report on the response of a forb community to chronic (long term) fertilization in a tidal salt marsh at Dipper Harbour on the New Brunswick coast of the Bay of Fundy. The response of *Plantago maritima*, *T. maritima* and other forbs is compared to that of a *S. patens* dominated community in the same marsh.

Methods

Study Site

The experiment was carried out in a tidal salt marsh at Dipper Harbour, situated on the New Brunswick coast of the Bay of Fundy (Fig. 1). At Dipper Harbour the amplitude of mean tides is 6 m and 8 m for large tides (Canadian Hydrographic Service 1995). Vegetation was described by Chmura et al. (1997). The distribution of graminoids is similar to that in salt marshes along the coast of the Northeast USA. *Spartina alterniflora* dominant in the lowest vegetated reaches of the marsh, *S. patens* dominant in the high marsh below *J. gerardii*, but *Puccinellia maritima* and *Festuca rubra* are common, although found in low abundance. Another notable exception is the presence of communities dominated by forbs, primarily *Plantago maritima* and *Triglochin maritima*. Forb-dominated assemblages occur not just in pannes, but in better drained soils of the marsh, usually at elevations between *S. patens* and *S. alterniflora.*

Experiment and Environmental Measurements

Permanent 70 cm x 70 cm plots were established haphazardly, a minimum of 3 m apart, in two plant communities. One community was dominated by *Plantago maritima* and *T. maritima*, and the other by *S. patens*. The ecological importance of species was assessed in late August 2005 and 2024, using point intercept (Roman, 2001) to determine the relative cover of species in experimental plots. (As this is a continuing experiment we avoided harvesting plants for biomass.)

Treatments consisted of biweekly fertilization during the growing seasons (early May through September) from 2005 to 2007. In 2008, treatments were reduced to monthly applications. Each application consisted of 30 g of Scott's Turfbuilder, a slow release fertilizer containing 29% N (5.3% ammoniacal N, 13.1% urea-N, 9.7% other water soluble N, and 0.6% water insoluble N); 2% P_2O_5, 12% K_2O, 11% S, 1%

water soluble Fe, and 0.5% Mn. When this formulation was no longer available we applied Scott's Super Turfbuilder, a slow release fertilizer containing 24% N (6.4% ammoniacal N, 9.9% urea-N, 7.1% other water soluble N, and 0.9% water insoluble N); 3% P_2O_5, 7% K_2O, and 7% S.

During growing seasons, soil pore water was collected from ≥ 15 cm depth by inserting a perforated plastic tube in the middle of each plot, as described by Yu & Chmura (2010). When no free pore water was available, the tube was inserted deeper into the soil, up to 30 cm depth. This step enabled retrieval of pore water from most plots, except for, occasionally, some of the *Plantago*-dominated ones. Salinity of soil pore water was measured using a hand-held refractometer (± 0.1).

Plot elevations were measured in 2024 and 2003 with a Sokkia GRX3 Real-Time Kinematic. GRX3 is an all-in-view constellation RTK GNSS receiver applied with the CGVD2013 geoid model, which provides elevation relative to sea level in real time. The post-survey accuracy observed was 0.47 cm in the vertical. Measurements taken at the four corners and the center of each plot were then averaged to represent plot elevation.

Statistical Analyses

All statistical analyses were performed with IBM SPSS 29. The effect of fertilization on species composition, and elevation change in plots was examined through a T-test. For species competition, the relative cover of forbs and graminoids was analyzed with a general linear model to test the effects of fertilization, salinity, distance from the creek, elevation, and all interactions.

Results

Environmental Data

Average salinity, elevations and distance from plots to the nearest creek are reported in Table 1 while individual plot measurements are reported in Tables 2 and 3. Average salinity of soil pore water was slightly higher in the forb than the *S. patens*-dominated plots. However, there was no significant difference between control and fertilized plots within the *S. patens*- or forb-dominated plots. Although plot elevations increased between 2003 and 2024, there was no significant difference between average elevations of fertilized and control plots in either year. The average distance to the nearest creek of the *S. patens*-dominated plots was more than twice that of the average distance to forb-dominated plots. This distance did not significantly vary between fertilized and control plots of either community.

Vegetation

By the end of the experiment a total of 13 species were encountered within the experimental plots (Tables 2 and 3). Point intercept measurements included the graminoids *Bolboschoenus maritimus*, *Puccinellia maritima, S. alterniflora*, and *S. patens* as well as the forbs *Atriplex patula, Glaux maritima, Limonium carolinianum, Plantago maritima, Argentina anserina (=Potentilla anserina), Salicornia maritima, Spergularia canadensis, Suaeda maritima*, and *Triglochin maritima*. In the originally forb-dominated plots there were notable declines in *Plantago maritima* and *T. maritima*, with increases in *S. patens*, *S. alterniflora* and *S. maritima*. Although the overall average species richness of forbs declined under both fertilization and control treatments in the forb plots, these differences were not significant (Table 4). There was even less variability in species richness in the *S. patens* plots (Table 4).

There was no change in the total cover of graminoid and forb species in the *S. patens*, but significant changes occurred with fertilization of the originally forb-dominated plots (Fig. 2). The average grass cover in the forb-dominated plots increased under both control and fertilization but the increase was not significant. However, under fertilization the forb-dominated plots had a significant reduction in forb cover – by nearly half.

Fig. 2 % cover of forbs and graminoids at beginning of experiment and after 20 years of fertilization of a) forb-dominated plots and b) Spartina patens dominated plots. The only significant difference is the decline in forb cover in the originally forb-dominated plots.

Neither elevation nor distance from the creek had a significant effect on the decreases in forbs in fertilized forb plots tested by a general linear model. Average soil porewater salinity, which was slightly higher in fertilized forb plots, was identified as a significant factor influencing the forb/ graminoid cover ratio. No interactive effect was observed from these results.

Discussion

We assume that increased N supplied by our experimental fertilization disproportionally benefited grasses in dealing with salinity stress, allowing them to out-compete forbs. A major mechanism that halophytes employ to deal with the osmotic stress of saline soils is the production of osmolytes. These are compounds that by accumulating in a plant's cytoplasm balance the osmotic potential of the Na^+ and

Cl^- ions that are taken up from the soil and accumulate in vacuoles of the cells (Slama et al 2015). There are three primary types of osmolytes quaternary ammonium compounds such as glycine betaine and proline, tertiary sulfonium compounds such as dimethylsulfoniopropionate, and soluble carbohydrates, i.e., sugars and sugar alcohols such as surcrose, mannitol and sorbitol (Jawahar et al. 2019). Nitrogen is an important element in both the quaternary ammonium osmolytes and the enzymes that produce them while soluble carbohydrates contain no nitrogen (Cavalieri & Huang 1983; Jawahar et al. 2019).

Hence, increasing the availability of reactive nitrogen confers a major advantage to those species dependent upon glycine betaine and proline. As the grasses *S. patens* and *S. alterniflora* are noted for their dependence on proline and glycine betaine (Cavalieri & Huang 1979. Hester et al. 2001) but also the forb *Suaeda maritima* for proline (Moghaieb et al. 2004), their increase in fertilized forb plots is most likely due to their access to increased reactive nitrogen (Cavalieri & Huang 1983). We note that salinity was the only environmental characteristic that helped explain the decrease in the forb/graminoid ratio.

In contrast, the most important osmolyte used by *Plantago maritima* is sorbitol (Ahmed et al. 1979) while *Triglochin maritima* seems to use both soluble carbohydrates and proline as osmolytes (Briens & Larher 1982). Thus, increased supply of reactive nitrogen through our fertilization would have conferred no advantage to the forbs, particularly with the increasing salinity observed. The exception is *S. maritima* which did increase, likely linked to its dependence upon glycine betaine and proline as osmolytes (Moghaieb et al. 2004).

If increased availability of reactive nitrogen favors grasses, we could postulate that the absence of similar forb communities from marshes at lower latitudes on the Northwest Atlantic coast could be related, in part to the historically higher supply of nitrogen there (Galloway et al. 2002). The coastline to the south of New Hampshire is highly developed and urbanized while the Bay of Fundy coast is predominantly rural (e.g., Wang et al. 2025). The predominance of urban land use would result in high nitrogen loading to estuarine waters (Wang et al. 2022; Galloway et al. 2002), perhaps conferring the same advantage to *S. alterniflora* and *S. patens* that dominate those marshes. Increased nitrogen loading would have begun with land clearance associated with European settlement (Chmura et al. 2004) and continue to increase with population growth. To test this theory by reducing nitrogen availability would present major challenges. However, the pollen and macrofossil record found in salt marsh sediments (Beecher & Chmura 2004; Daoust et al. 1996; Chmura et al. 2001) dating prior to European colonization could reveal prior importance of forb communities like those on the coast of eastern Canada.

Declarations

Competing interests:

The authors have no financial or proprietary interests in any material discussed in this article.

Author Contributions:

GLC: conceptualization, methodology, investigation, funding acquisition, writing—original draft, and writing—review and editing. YW: investigation, data analyses, review and editing.

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Data Availability:

All data is reported within the manuscript.

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Tables

Table 1. Average (avg) and standard deviation (sd) of environmental measurements from experimental plots.

	Spartina patens				Forb			
	Control		Fertilized		Control		Fertilized	
parameter	avg	sd	avg	sd	avg	sd	avg	sd
Distance from nearest creek (m)	16.5	9.7	12.3	7.0	6.5	6.8	3.5	2.9
Salinity	26.5	3.6	26.4	3.3	28.3	0.8	29.0	2.1
2024 elevation (cm)	339	6	337	8	337	3	344	10
2003 elevation (cm)	326	2.1	325	2.8	328	4	324	7
elevation change (cm)	12.2	4.5	11.6	5.1	9	1	20	7

Table 2 Percent cover of species in forb-dominated plots and elevation above sea level (m) at beginning and end of experiment. Soil porewater salinity (PSU) is averaged over experiment and distance to nearest creek (m) measured in 2024.

Treatment	Control						Fertilized							
Year	2005			2024			2005				2024			
Plot	5	6	8	5	6	8	1	3	4	7	1	3	4	7
Elevation above sea level	3.31	3.30	3.25	3.41	3.38	3.35	3.14	3.31	3.28	3.24	3.32	3.51	3.41	3.53
Salinity				29.2	28.3	27.2					26.3	31.3	29.5	28.8
Distance to creek				4.0	3.1	2.2					1.3	5.0	1.0	6.9
graminoids														
S. patens	0	0	0	39.2	5.1	32.9	0	0	0.7	0	54.8	8.2	8.3	1.3
S. alterniflora	2.3	3.7	1.8	0	3.4	3.9	0.7	11.2	4.1	13.2	45.2	35.3	8.3	37.2
Puccinellia maritima	0	0	0	0	0	11.8	19.0	25.8	9.5	0.0	0	15.3	9.2	17.9
Bolboschoenus maritimus	0	0	0	0	0	0	0	0	0	0	0	3.5	0	0
forbs														
Plantago maritima	53.9	53.3	64.3	41.8	28.8	43.4	49.0	39.3	47.3	52.9	0	3.5	25.7	5.1
Triglochin maritima	29.7	32.6	25.0	12.7	55.9	6.6	2.7	8.4	29.1	26.5	0	0	0.9	3.8
G. maritima	10.9	9.6	2.7	0	0	0	0.7	9.0	0.7	0	0	0	0	0
L. carolinianum	1.6	0.7	3.6	5.1	6.8	0	0	0	2.0	1.5	0	0	11.9	0
P. anserina	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
Salicornia maritima	0.8	0	0	0	0	0.0	2.7	0.6	2.0	0	0	0	0.9	0
S. canadensis	0	0	0	0	0	0.0	1.4	0	0	0	0	3.5	11.9	9.0
Suaeda maritima	0	0	2.7	1.3	0	1.3	23.1	4.5	4.7	3.7	0	28.2	22.9	21.8
A. patula	0	0	0	0	0	0	0.7	1.1	0	2.2	0	2.4	0	3.8

Table 3 Percent cover of species in *Spartina patens* -dominated plots and elevation above sea level (m) at beginning and end of experiment. Soil porewater salinity (PSU) is averaged over experiment and distance to nearest creek (m) measured in 2024.

Treatment	Control								Fertilized					
Year	2005				2024				2005			2024		
Plot	1	4	6	8	1	4	6	8	2	3	5	2	3	5
Elevation above sea level	3.24	3.26	3.26	3.29	3.34	3.35	3.36	3.48	3.24	3.23	3.23	3.33	3.31	3.34
Salinity					29.6	26.2	28.7	21.5				27.8	27.8	28.3
Distance to creek					22.6	20.4	21.2	2.0				17.1	13.3	16.7
graminoids														
S. patens	91.1	100	82.8	74.2	100	67.9	70.8	94.7	72.0	96.0	98.6	60.0	81.8	83.7
S. alterniflora	0	0	0	1.03	0	0	0	0	0	0	0	0	0	0
forbs														
Plantago maritima	3.8	0	0	3.1	0	0	6.3	5.3	0	1.3	0	5.0	0	0
Triglochin maritima	0	0	0	0	0	0	18.8	0	0	0	0	0	0	0
G. maritima	1.3	0	11.5	14.4	0	1.9	2.1	0.00	3.0	0	0	0	0	0
L. carolinianum	0	0	0	0	0	0	0	0	0	0	0	0	0	7.0
Salicornia maritima	1.3	0	0	0	0	1.89	0	0	2.0	0	0	6.7	6.8	2.3
Suaeda maritima	2.5	0	3.4	7.2	0	7.5	2.1	0	9.0	1.3	0	15.0	2.3	7.0
A. patula	0	0	2.3	0	0	20.8	0	0	14.0	1.3	1.4	13.3	9.1	0

Table 4 Species richness in plots designated as control and fertilized at the beginning of the experiment in 2005 and when sampled by point intercept in 2024.

			all		forbs		graminoids	
dominant taxa	treatment	year	avg	sd	avg	sd	avg	sd
Spatina patens	Control	2005	3.8	1.6	2.5	1.5	1.3	0.4
Spatina patens	Fertilized	2005	3.3	1.3	2.7	1.2	1.0	0.0
Spatina patens	Control	2024	3.3	1.8	2.3	1.8	1.0	0.0
Spatina patens	Fertilized	2024	3.8	1.1	3.3	0.5	1.0	0.0
forb	Control	2005	6.0	0.8	5.0	0.8	1.0	0.0
forb	Fertilized	2005	8.8	1.6	6.8	1.1	2.0	0.7
forb	Control	2024	5.8	0.8	3.7	0.5	2.0	0.8
forb	Fertilized	2024	7.5	3.2	4.5	2.7	3.0	0.7

Figures

Figure 1

Location of Dipper Harbour (red circle) in context of broader coastal regions. Image Landsat / Copernicus Data SIO, NOAA, US Navy, NGA, GEBCO, ldeo-Coumbia, NSF, NOAA.

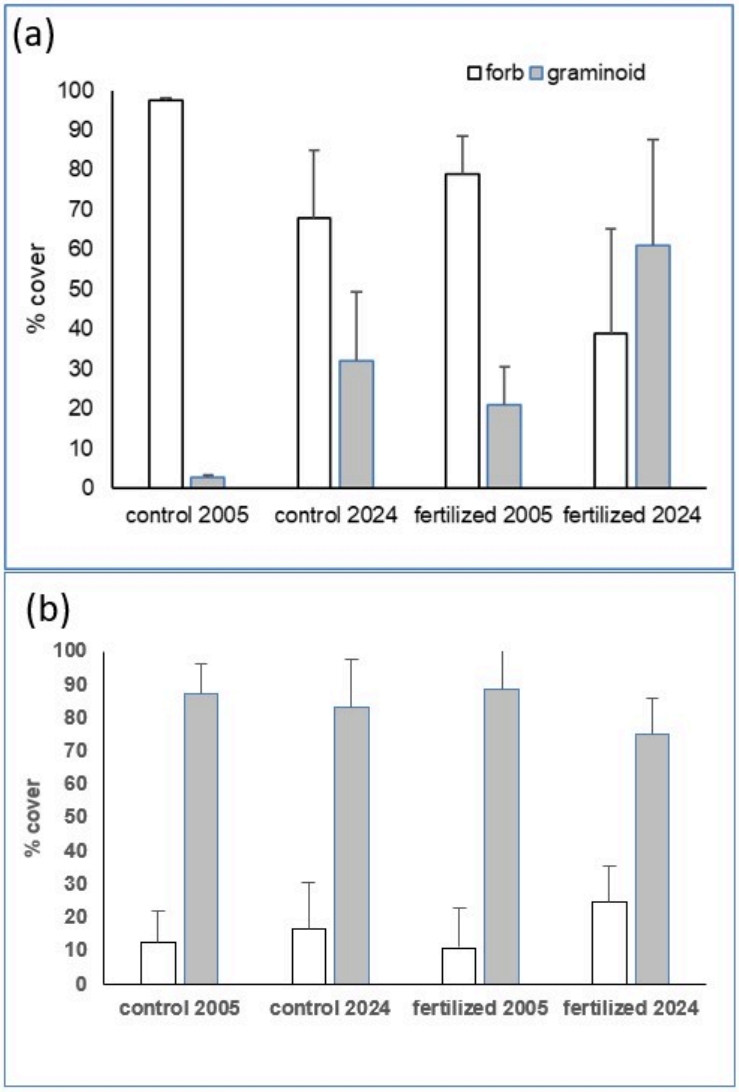

Figure 2

% cover of forbs and graminoids at beginning of experiment and after 20 years of fertilization of a) forb-dominated plots and b) Spartina patens dominated plots. The only significant difference is the decline in forb cover in the originally forb-dominated plots.